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Body size, extinction events, and the early Cenozoic record of veneroid bivalves: a new role for recoveries?

Rowan Lockwood

Abstract.—Mass extinctions can play a role in shaping macroevolutionary trends through time, but the contribution of recoveries to this process has yet to be examined in detail. This study focuses on the effects of three extinction events, the end-Cretaceous (K/T), mid-Eocene (mid-E), and end-Eocene (E/O), on long-term patterns of body size in veneroid bivalves. Systematic data were collected for 719 species and 140 subgenera of veneroids from the Late Cretaceous through Oligocene of North America and Europe. Centroid size measures were calculated for 101 subgenera and global stratigraphic ranges were used to assess extinction selectivity and preferential recovery. Veneroids underwent a substantial extinction at the K/T boundary, although diversity recovered to pre-extinction levels by the early Eocene. The mid-E and E/O events were considerably smaller and their recovery intervals much shorter. None of these events were characterized by significant extinction selectivity according to body size at the subgenus level; however, all three recoveries were strongly size biased. The K/T recovery was biased toward smaller veneroids, whereas both the mid-E and E/O recoveries were biased toward larger ones. The decrease in veneroid size across the K/T recovery actually reinforced a Late Cretaceous trend toward smaller sizes, whereas the increase in size resulting from the Eocene recoveries was relatively short-lived. Early Cenozoic changes in predation, temperature, and/or productivity may explain these shifts.

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Introduction

Mass extinctions can influence large-scale patterns in the fossil record by reinforcing, disrupting, or in some cases, even establishing trends. Few extinction events have a discernible effect on long-term trends, but in situations in which they do, extinction selectivity is presumed to play a major role (Norris 1991; Saunders et al. 1999). Although recovery intervals have received little attention until recently, preferential (or biased) recovery can affect both the direction and magnitude of evolutionary and ecomorphological change. Comparing patterns of selectivity in a single clade across multiple events may shed light on the connections among extinction, recovery, and long-term trends. The purpose of this study is to examine extinction selectivity and preferential recovery with respect to body size in veneroid bivalves across the end-Cretaceous and Eocene extinctions. Questions to be addressed include (1) Do these events show any evidence of extinction selectivity or preferential recovery according to veneroid size? (2) Does selectivity differ between extinction and recovery intervals or among events? and (3) What effects (if any) do these events have on long-term patterns of veneroid size?

Body size is considered one of the most fundamental attributes of organisms, reflecting interactions among developmental, life history, physiological, and ecological processes (McKinney 1990; Blackburn and Gaston 1994). Large-scale patterns associated with body size, including ''Cope's rule,'' have been documented across a variety of clades and time intervals (Stanley 1973; see review *in* Jablonski 1996, 1997; Alroy 1998; among others). The effects of extinction events on these trends are rarely investigated, although the broader question of whether extinctions are size selective has received considerable attention.

A clear-cut relationship between body size and extinction probability has proved difficult to document in the fossil record. Studies of background extinction in the fossil record seem to show no significant relationship between body size and survivorship (see discussion of Hallam 1975 *in* Jablonski 1996; Budd and Johnson 1991), with the exception of Stanley's (1986, 1990) data on Late Pliocene bi-

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valves from California and Japan. The concept that mass extinctions selectively eliminate large taxa is intuitively appealing, but rarely substantiated (LaBarbera 1986; Raup 1995). Global data for bivalve genera show no evidence of size selectivity across the K/T mass extinction (Jablonski and Raup 1995; Jablonski 1996). Similar patterns have been documented in European bivalves across the end-Triassic extinction (McRoberts and Newton 1995; McRoberts et al. 1995) and North American mammals across the late Eocene extinction (Van Valkenburgh 1994). Although size selectivity is often cited for K/T dinosaurs and birds (Russell 1977; Clemens 1986), it is unclear to what extent these patterns represent clade-specific extinction (Jablonski 1996). Perhaps the best-documented case of size selectivity in the fossil record is the preferential extinction of large planktonic foraminifera across the K/T extinction (Norris 1991; Arnold et al. 1995).

The present study focuses on the late Mesozoic and early Cenozoic record of body size in three closely related superfamilies of heterodont bivalves: the Veneroidea, Arcticoidea, and Glossoidea (collectively referred to here, for simplicity's sake, as veneroids). The veneroids are infaunal, suspension-feeding bivalves that experienced a remarkable radiation during the last 65 Myr and are abundant in modern shallow marine environments (Palmer 1927; Cox 1969; Canapa et al. 1996, 1999; Harte 1998a,b; Passamonti et al. 1998, 1999; Coan et al. 2000).

The extinction events examined in this study differ considerably according to duration, magnitude, and causal mechanism. The K/T extinction, which occurred at 65 Ma, is one of the ''Big Five'' mass extinctions and has received considerable attention, primarily because of evidence that it was caused by a bolide impact (see papers in Ryder et al. 1996). The Eocene–Oligocene transition was one of the most severe events faced by marine invertebrates during the Cenozoic (Prothero et al. 2003). When this event is examined in detail, at least two minor pulses of extinction can be recognized: one at the end of the middle Eocene (37 Ma, mid-E) and one at the end of the Eocene (33.7 Ma, E/O) (Ivany et al. 2003a). Possible causes of both of these extinctions include climate change (Hansen 1987; Ivany et al. 2003a) and sea level fluctuation (Dockery 1986; Dockery and Lozouet 2003).

Methods

This study involved the collection of systematic data for 719 veneroid species (representing 140 subgenera) recorded from Late Cretaceous to Oligocene deposits in North America and Europe. Data collection was limited to extratropical regions to avoid the poor preservation and minimal sampling associated with tropical environments during this time. Taxonomic identifications were based on personal observation and alpha-taxonomic information available in the literature. For a more detailed description of systematics and sampling, see Lockwood (2004).

Size data were obtained for 1236 specimens (representing 101 subgenera) sampled from both field and museum collections. Specimens were photographed in two orientations (lateral and cross-sectional [Fig. 1]) and 100 equally spaced points were digitized around each outline using Optimas 5.2 for Windows. Centroid size was calculated in both lateral (C_l) and cross-sectional (C_c) orientations as the square root of the sum of squared distances of the set of landmarks from their centroid (Bookstein 1991). Centroid size is the only measure of size to be uncorrelated with shape in the absence of allometry and is increasingly used in morphometric studies of fossil taxa (e.g., Roopnarine and Beussink 1999; Anderson 2001; Roopnarine and Tang 2001). Centroid size measures were significantly positively correlated with traditional linear measures (including shell length and height) (all Spearman $R_{100} = 0.81$; $p < 0.0000001$). Given the tight correlations among these size measures and the advantages associated with centroid size, I opted to use the latter for the remainder of this study. I combined the two measures of centroid size into a single measure by calculating their geometric mean (C_{geo}) (Stanley 1986, 1990). I used the largest specimen available for each species to ensure that I was measuring adult, rather than juvenile, specimens (Stanley 1973; Jablonski 1997).

I compiled stratigraphic occurrences from

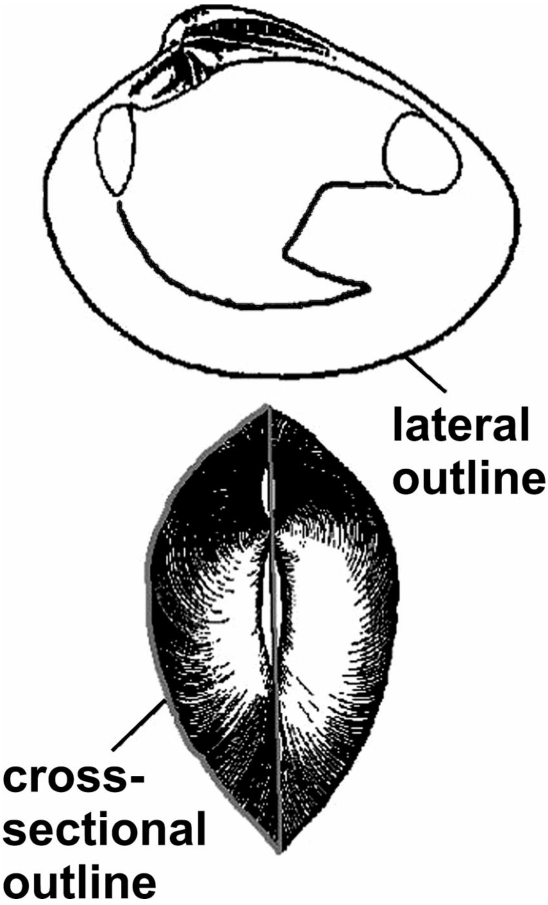

FIGURE 1. Lateral and cross-sectional size measures. One hundred equally spaced points were digitized around the shell outline in two orientations: lateral and cross-sectional.

fieldwork, museum collections, and the literature for 140 subgenera. First (FAD) and last (LAD) appearance data were established for each subgenus on the basis of global occurrence data. Stratigraphic range data for subgenera are available in Lockwood (2004). The Late Cretaceous through Oligocene was divided into 28 intervals, which range in duration from 2 to 4 Myr, and make it possible to compare diversity across time intervals of roughly similar durations. These intervals were designed to coincide with major chronostratigraphic and biostratigraphic boundaries, whenever possible.

Subgeneric diversity was calculated by counting boundary-crossing taxa (Foote 2000; see also Harper 1975; Bambach 1999). Estimated per-taxon rates of extinction (q) were calculated by using the number of taxa that range completely through an interval relative to the total number that range out of the interval, as in Foote (2000). Global stratigraphic ranges were used to categorize subgenera as victims, survivors, or new taxa for the K/T, mid-E, and E/O events. Victims are subgenera that went extinct, survivors are subgenera that survived, and new taxa are subgenera that originated during the recovery interval. I defined recovery as the interval required for veneroid diversity to reach pre-extinction levels. I compared the means of victims and survivors to assess extinction selectivity and the means of survivors and new taxa to assess preferential recovery.

All of the species representing a subgenus throughout its geographic (in North America and Europe) and stratigraphic range were pooled to calculate the mean of each size measure for each subgenus. Kolmogorov-Smirnov one-sample tests of normality revealed no significant deviation in the distribution of any of the size measures from a normal distribution after adjustment for multiple comparisons (all $D_{100} > 0.14$; $p > 0.05$). Subsequent analyses of these measures used parametric statistics, except when otherwise stated. Sequential Bonferroni adjustment was applied to each independent pool of statistical analyses, to adjust for multiple comparisons (Rice 1989).

Results

Veneroid Diversity

Patterns of veneroid diversity from the Late Cretaceous through early Cenozoic (Fig. 2A) are similar to those documented for bivalves as a whole (Miller and Sepkoski 1988; Raup and Jablonski 1993). Veneroid diversity increased throughout the Late Cretaceous and early Cenozoic, with the exception of a minor plateau in the Eocene. A major extinction occurred at the K/T boundary, along with very minor extinctions in the early Turonian, at the end of the middle Eocene, and at the end of the Eocene (Fig. 2B). The K/T extinction was slightly more severe for veneroids (79% decrease in subgeneric diversity, 81% extinction) than for bivalves in general (Raup and Jablonski 1993). This may relate to the fact that ma-

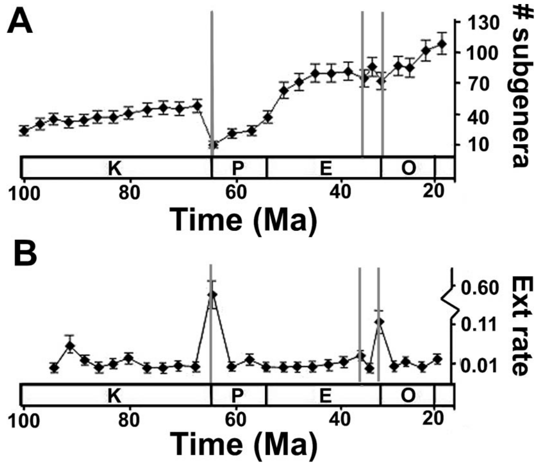

FIGURE 2. A, Diversity patterns in veneroids. Global subgeneric diversity measured as the number of taxa crossing boundary intervals. Error bars represent the square root of the number of taxa crossing each boundary (Foote 1993), derived from the standard error of a Poisson variable. The three gray lines represent the K/T, mid-E, and E/O extinctions. B, Estimated per-taxon extinction rate (q) measured by using the number of taxa that range completely through an interval relative to the total number that cross into the interval (Foote 2000). Error bars are approximate and represent ± 1 SD calculated from the 95% confidence intervals of a proportion (M. Foote, personal communication, 2000). The three gray lines represent the K/T, mid-E, and E/O extinctions.

rine suspension feeders such as veneroids tended to suffer greater extinction at the K/T than deposit feeders (Sheehan and Hansen 1986; Jablonski and Raup 1995). The K/T recovery was relatively rapid and veneroid diversity reached pre-extinction levels by 53 Ma. This contrasts with Hansen's (1988) data for Gulf Coast bivalve species, which indicate that diversity did not rebound fully before the E/O event (Hansen 1988; see also Stanley 1990). Hansen's results may conflict with mine simply because of the different taxonomic levels and spatial scales used in the two analyses. It is worth noting, however, that the effects of the K/T were not protracted for the majority of marine organisms and paleocommunities (Arnold et al. 1995; Sheehan et al. 1996; Jablonski 1998; Heinberg 1999).

Similar to Gulf Coastal Plain mollusks (Dockery 1998), veneroids show little genus-level extinction across the Paleocene/Eocene boundary (Fig. 2). A very minor extinction occurred at the end of the middle Eocene (37 Ma; 8.5% decrease in subgeneric diversity, 8.5% extinction) and a second, slightly more severe extinction at the end of the Eocene (33.7 Ma; 16.3% decrease in subgeneric diversity, 18.6% extinction). Background extinction levels (excluding the K/T, mid-E, or E/O events) average 4.1% for veneroid subgenera throughout this interval. Bootstrap resampling (1000 random resamplings with replacement) yielded 95% confidence intervals ranging from 1.98% to 6.76%, indicating that the extinction levels documented for the K/T, mid-E, and E/O events exceed background levels. The recovery intervals following the mid-E and E/O events were considerably shorter than the K/T recovery and were complete by 35.4 Ma and 31 Ma, respectively. Comparing the timing and magnitude of veneroid extinctions with Eocene extinctions in other mollusks is complicated by a scarcity of published data with comparable taxonomic and spatial scaling. Dockery's and Hansen's studies of Gulf Coast molluscan faunas remain the most often cited studies (Dockery 1984, 1986; Hansen 1987, 1988, 1992; Haasl and Hansen 1996; Dockery and Lozouet 2003). Both of these data sets document a major extinction of mollusk species at the mid-E boundary and a larger, more abrupt extinction at or near the E/O boundary. Haasl and Hansen (1996) argued that the immediate appearance of a high diversity fauna after the E/O boundary demonstrates that the recovery was complete by the earliest Oligocene. Their estimate of recovery duration agrees well with the patterns documented in this study.

Extinction Selectivity and Preferential Recovery

K/T.—Veneroid size frequency distributions before the K/T extinction differ considerably from those after the K/T recovery (Fig. 3A,B), suggesting that this event may be size selective at the subgenus level. To determine whether this selectivity is associated with the extinction itself or the subsequent recovery, I compared victims with survivors and survivors with new taxa across the K/T boundary. I found no evidence of size-selective extinction across the K/T event (Table 1, Fig. 4A). The recovery was, however, biased toward smaller veneroids. New taxa are significantly smaller

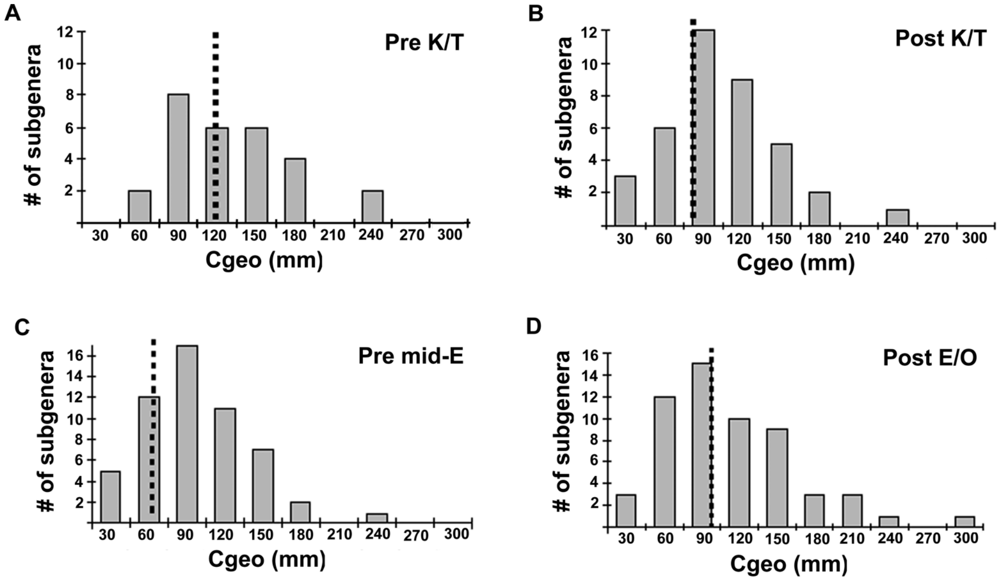

FIGURE 3. Size frequency distributions for veneroid subgenera that occur before the K/T extinction (A), after the K/T recovery (B), before the mid-E extinction (C), and after the E/O recovery (D). Mean centroid size (C_{geo}) for each interval is indicated by the dashed line on each plot.

than survivors. These patterns remain robust when size is partitioned into lateral and cross-sectional measures. There is no indication of extinction selectivity in either measure, and preferential recovery toward smaller taxa is evident in both lateral and cross-sectional measures, although the signal is stronger in the former.

These selectivity analyses are based on means calculated by pooling all of the species representing a subgenus throughout its stratigraphic and geographic range (in North America and Europe). To determine whether this pooling affected the results, I also compiled subgeneric means at the stage level. To assess extinction selectivity, I calculated the means of victims and survivors solely on the basis of Maastrichtian species and to test for preferential recovery, I calculated the means of survivors and new taxa solely on the basis of Paleocene species. The resulting trends were in the same direction, although not always statistically significant, as those outlined above.

Mid-E.—Turning to the Eocene events, size frequency distributions record a very slight increase in veneroid size across these intervals (Fig. 3 C,D). The mid-E extinction showed no selectivity according to subgeneric size, regardless of how size was measured (Table 1, Fig. 4B). The recovery was, however, size biased. New taxa are significantly larger than survivors when size is measured as geometric mean, centroid size in lateral orientation, or

TABLE 1. Extinction selectivity (Ext) and preferential recovery (Rec) according to veneroid size across the K/T, mid-E, and E/O events. Statistically significant results are in boldface.

	KT		mid-E		E/O	
	Ext	Rec	Ext	Rec	Ext	Rec
C_{geo}	$t_{19,9} = 0.35$, $p = 0.73$	**$t_{9,29} = 1.99$,** **$p = 0.05$**	$t_{6,49} = -0.66$, $p = 0.51$	**$t_{49,2} = -2.90$,** **$p = 0.005$**	$t_{5,46} = -1.08$, $p = 0.29$	**$t_{46,11} = -2.6$,** **$p = 0.01$**
C_l	$t_{19,9} = -0.24$, $p = 0.81$	**$t_{9,29} = 2.90$,** **$p = 0.006$**	$t_{6,49} = -0.99$, $p = 0.32$	**$t_{49,2} = -3.64$,** **$p = 0.0007$**	$t_{5,46} = -0.81$, $p = 0.42$	**$t_{46,11} = -2.85$,** **$p = 0.006$**
C_c	$t_{19,9} = 0.18$, $p = 0.86$	**$t_{9,29} = 2.18$,** **$p = 0.04$**	$t_{6,49} = -0.48$, $p = 0.63$	**$t_{49,2} = -1.97$,** **$p = 0.05$**	$t_{5,46} = -1.18$, $p = 0.24$	$t_{46,11} = -1.77$, $p = 0.08$

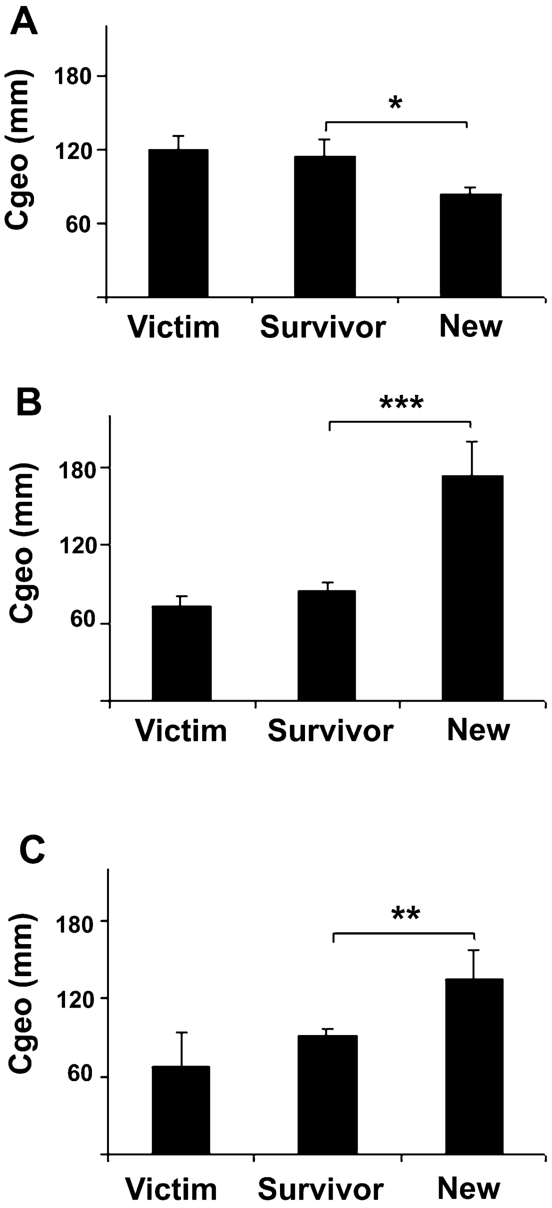

FIGURE 4. Mean (±SE) centroid size (C_{geo}) of victims, survivors, and new taxa across the K/T, mid-E, and E/O events. A, K/T event. No significant difference between victims and survivors. New taxa are significantly smaller than survivors ($t_{9,29} = 1.99$; $p = 0.05$). B, Mid-E event. No significant difference between victims and survivors. New taxa are significantly larger than survivors ($t_{49,2} = -2.90$; $p = 0.005$). C, E/O event. No significant difference between victims and survivors. New taxa are significantly larger than survivors ($t_{46,11} = -2.6$; $p = 0.01$).

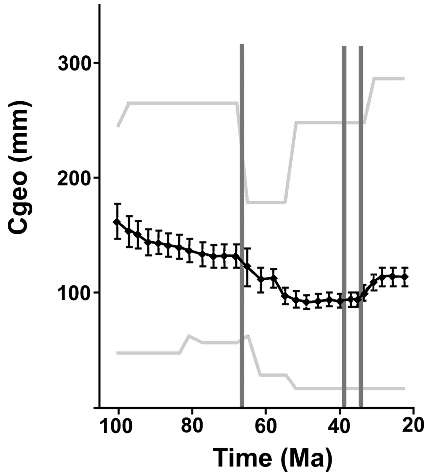

FIGURE 5. Mean (±SE) centroid size (C_{geo}) through time. Gray lines represent the maximum and minimum values for C_{geo} through time. The three dashed lines represent the K/T, mid-E, and E/O extinctions.

centroid size in cross-sectional orientation. The recovery results should be treated with caution, owing to the extremely small sample of new taxa in this analysis (n = two subgenera classified in different superfamilies).

E/O.—Finally, I found no evidence of extinction selectivity at the E/O according to subgeneric size, regardless of the size measure examined (Table 1, Fig. 4C). Similar to the mid-E, the E/O recovery was biased toward larger taxa. New taxa are significantly larger than survivors when size is measured as geometric mean and as centroid size in lateral orientation. There is a tendency for new taxa to be larger than survivors when centroid size is measured in the cross-sectional orientation; however, the difference is not statistically significant.

Body Size in Veneroids through Time

General Patterns.—To examine the effects of the K/T, mid-E, and E/O events on long-term patterns of veneroid size, I plotted the mean (±SE) of centroid size (C_{geo}) through time (Fig. 5). All of the species representing a subgenus throughout its geographic (in North America and Europe) and stratigraphic range were pooled to calculate the mean of each size measure for each subgenus, and all subgenera crossing a boundary contributed to the calculation of the mean for that boundary. This range-through approach assumes that the size of a subgenus is unlikely to vary appreciably relative to the size among subgenera, an assumption that is supported by the fact that centroid size variation is statistically smaller within veneroid subgenera than among subgenera ($F_{62,326} = 4.34$; $p < 0.001$) throughout this interval. This technique is not without its limitations (explored in Foote 1991, 1994); however, in this particular case it is likely to underestimate rather than overestimate shifts in size across these boundary events. Veneroid size decreased gradually throughout the Late Cretaceous. The K/T recovery, which was significantly biased toward smaller taxa, produced a marked decrease in size that continued until 51.8 Ma. In fact, veneroid size before the K/T (averaged across the ten million years leading up to the boundary) is significantly larger than after the K/T (averaged across the ten million years following the boundary) (Mann-Whitney $U_{3,4} = 2.12$; $p = 0.03$). These results are remarkably robust, regardless of the time intervals included in the comparison. The K/T recovery appears to have reinforced and even accelerated an established trend toward decreasing size.

Veneroid size remained relatively constant until the E/O event, when it began to increase slightly. This increase leveled off by the middle Oligocene. A comparison of veneroid size before the Eocene events (averaged across the ten million years leading up to the boundary) versus size after the Eocene events (averaged across the ten million years following the E/O recovery) documents a significant increase (Mann-Whitney $U_{4,4} = -2.31$, $p = 0.029$), regardless of the time intervals used in the comparison. The Eocene recovery intervals reversed the earlier trend toward decreasing body size and initiated a short-lived interval of increasing body size. When size is partitioned into lateral and cross-sectional components, these patterns remain unchanged. Unfortunately, given the limited sample sizes of veneroid subclades (average of four subclades, five subgenera per subclade per interval), it was not possible to characterize these trends as driven versus passive.

Effects of Sampling, Preservation, Taxonomic Level, and Phylogenetic Bias.—Large taxa in the fossil record are more likely to be sampled (Valentine 1989; Kidwell and Bosence 1991) and identified than small taxa. Indeed, the incidence of small taxa increases dramatically when sediments are bulk-sampled or when intervals are particularly well sampled. Although sampling could account for the shifts in mean size documented here, two pieces of evidence indicate that it is not exerting substantial influence. First, sampling, quantified as the number of localities compiled for each time interval, is not correlated with size in this study. Correlation between the first-order differences of size and sampling revealed no significant relationship ($r_{26} = 0.01$; $p = 0.97$). Second, Sohl and Koch (1983, 1984, 1987) bulk-sampled several localities in the latest Maastrichtian and these occurrences are included in this study. If sampling were affecting these results, I would expect size to decrease sharply within the interval including the Sohl and Koch data. Instead, it remains constant.

Preservation is also unlikely to yield these patterns. Larger taxa are more likely to be preserved than small taxa (Kidwell and Bosence 1991), and small taxa are more likely to be recorded from well-preserved intervals. Preservation may help to explain the small size of Eocene veneroids, but it cannot explain the size decrease immediately after the K/T (which occurs during a time of poor preservation, characterized by dissolution of shell material and moldic preservation) or the increase after the E/O (which occurs during a time of good preservation, characterized by preservation of original aragonitic shell material). Moreover, preservational bias tends to affect the smallest tail of the bivalve size distribution (<2 mm in length [see for example Staff et al. 1986 in Texas bays]), as opposed to the mean sizes of veneroids documented throughout this interval (majority > 10 mm in length).

It is important to emphasize that the present study was carried out at the subgeneric taxonomic level. Because many of the predictions surrounding body size and extinction vulnerability are based on life-history traits that are relevant at the population or species level, it is worth considering whether the choice of taxonomic level is affecting these results. Although preferential recovery at the subgenus level may well indicate selectivity at the species level, a lack of extinction selectivity at the subgenus level does not necessarily indicate a lack of selectivity at the species level within individual lineages (see, for example, Smith and Roy 1999). The fossil record of veneroids at the species level is so limited during this interval that species-level analyses are simply not feasible. One potential way to explore the question of species level patterns would be to reanalyze selectivity within species-poor subgenera, presuming that the latter would be more likely to mimic species-level patterns. Species richness of veneroid subgenera across this interval varies from one to 30 (mean = 4.23 ± 4.95) and shows no correlation with size ($r_{25} = 0.09$; $p = 0.68$). When the selectivity analyses were redone for species-poor taxa (defined as subgenera containing fewer than the mean number of species), the only result that changed was the K/T recovery. The recovery was still biased toward small subgenera, but the bias was no longer statistically significant (C_{geo} $t_{7,25} = 1.24$, $p = 0.22$), in large part because of a decrease in sample size.

Phylogenetic bias could produce these shifts in size, if the K/T and Eocene recoveries represented radiations of single clades of small and large veneroids, respectively. Direct examination of phylogenetic bias requires a well-resolved phylogeny (Harvey and Pagel 1991), which is currently unavailable for veneroids. As an alternative, I tested for the effects of taxonomic sorting by comparing patterns within the three superfamilies examined in this study. When I reexamined extinction selectivity and preferential recovery within each of the three superfamilies, I found identical patterns of preferential recovery in each, although differences between survivors and new taxa were not always statistically significant owing to a reduction in sample size. When I plotted mean size through time for each superfamily, I also found very similar patterns. The gradual decrease in size in the Late Cretaceous (i.e., before the K/T extinction) is driven by arcticoid subgenera, but the K/T through Oligocene patterns are almost identical in the three superfamilies. This indicates that recovery-driven changes in size are not simply the result of sorting, at least at the superfamily level.

Discussion

Body Size and Extinction Vulnerability

The lack of size-selective extinction documented in this study corroborates past conclusions about mass extinctions in fossil mollusks (Jablonski and Raup 1995; McRoberts and Newton 1995; McRoberts et al. 1995; Jablonski 1996). In fossil marine invertebrates, dispersal ability and geographic range appear to be much better predictors of extinction vulnerability than body size.

Preferential Recovery According to Size

The K/T, mid-E, and E/O recoveries are all significantly biased with respect to veneroid size. Early recovery intervals after mass extinctions are sometimes characterized by ''disaster'' taxa, abundant species with unusually small body sizes. This pattern, termed the ''Lilliput'' phenomenon (Erwin 1998), has been documented for paleocommunities immediately following the Ordovician (Kaljo 1996), Silurian (Kaljo 1996), end-Permian (Gobbett 1973), end-Cenomanian (Harries 1993), and K/T (Håkansson and Thomsen 1999) events. The reduction in size is generally short-lived and restricted to a handful of opportunistic taxa. The protracted nature of the veneroid size decrease and the fact that the subgenera responsible do not appear to be opportunists or ecological generalists makes it unlikely that the patterns documented in this study are an example of the ''Lilliput'' phenomenon. In contrast to the K/T, the Eocene recovery intervals are biased toward larger veneroids. Few authors have explored body size patterns across the E/O transition, although Hickman (2003) did document an increase in the size of chemoautotrophic thyasirid bivalves from the Pacific Northwest.

Why Do Changes in Veneroid Size Occur Throughout This Interval?

Body size in veneroids shows a very clear pattern of decrease associated with the K/T recovery and minor increase associated with the Eocene recoveries. The K/T recovery appears to reinforce and even accelerate a trend toward smaller size already established by the Late Cretaceous. Several factors may be contributing to the patterns documented in this study and are considered below.

Predation.—Large size in bivalves is sometimes considered a refuge against predation (Boulding 1984; Vermeij 1987). If predation pressure is influencing these patterns, then the decrease in veneroid size throughout the Late Cretaceous should coincide with a decrease in predation and the increase in veneroid size across the Eocene events should coincide with an increase in predation. Kelley and Hansen's (1996) data on gastropod drilling from the late Mesozoic to early Cenozoic of the coastal plain allow me to test this hypothesis, albeit only for gastropod predators. Their data document an increase in gastropod predation immediately after the K/T extinction and a slightly smaller increase across the E/O event. Whereas the Eocene data fit the prediction, the Late Cretaceous patterns are completely contrary, suggesting that gastropod predation is unlikely to be driving this pattern.

Climate Change.—Size is commonly thought to vary with temperature in modern bivalves and latitude is often used as a proxy for temperature when this variation is examined interspecifically. Perhaps the most extensive data set available for modern bivalves has been compiled by Roy and others for Eastern Pacific taxa (Roy et al. 1998, 2000, 2002; Roy and Martien 2001). Extensive analyses reveal no straightforward, linear relationship between mean size and latitude, although a positive (nonsignificant) correlation between body size and latitude does exist in several temperate marine bivalve lineages. If that is the case, then given the extratropical distribution of the data compiled in this study, temperature increases in the early Cenozoic and decreases across the E/O transition could account for the pattern documented in this study. This possibility is further supported by the preferential extinction of warm-water taxa at the E/O transition (Hickman 1980; Hansen 1987; see papers in Prothero and Berggren 1992 and in Prothero et al. 2003).

Our understanding of temperature changes throughout the late Mesozoic and early Cenozoic has improved dramatically during the past decade and the reader is referred to recent compilations for additional information (Aubry et al. 1998; Prothero et al. 2003; Wing et al. 2003). The Late Cretaceous and early Cenozoic were, very generally speaking, dominated by warm climates, which culminated in the Paleocene-Eocene Thermal Maximum (PETM), widely recognized as one of the most rapid intervals (<200,000 years) of extreme warming in the Phanerozoic (Bains et al. 1999; Zachos et al. 2001). The middle Eocene marks the transition from ''greenhouse'' to ''icehouse'' conditions, with gradual cooling beginning at approximately 50 Ma (Zachos et al. 1994). Temperature shifts do tend to track changes in veneroid size (Fig. 5) across this interval, but the timing is somewhat problematic. Maximum warming during this interval (PETM) occurs at approximately 55 Ma, ten million years *after* the decrease in veneroid size associated with the K/T recovery begins. Similarly (but perhaps not as troubling), a minor lag exists between the onset of ''icehouse'' cooling at approximately 37 Ma and the increase in veneroid size associated with the Eocene recoveries (33.7 Ma). It is interesting to note that the increase in veneroid size does appear to coincide with an increase in seasonality (Ivany et al. 2003b).

Changes in Productivity.—Nutrient availability and primary productivity are thought to scale positively with body size in modern marine invertebrates (Jones et al. 1989; Allmon et al. 1992; Palmer 1992). If trends in veneroid size are linked to productivity, I would expect to see a steady decline in productivity during the Late Cretaceous, a drop in productivity across the K/T boundary, little change in the early Paleogene, then an increase across the E/O boundary.

The Late Cretaceous is characterized by normal levels of productivity until the K/T boundary event (D'Hondt et al. 1998). Several authors have documented a breakdown in the C^{13} gradient immediately after the K/T bolide impact, which has been interpreted as a sudden decrease in productivity (Hsü 1986; Zachos and Arthur 1986). A shift in C^{13} ratios is also recorded across the PETM (Katz et al. 1999, among others), which may reflect elevated global primary productivity (Bains et al. 2000); however, neither the microfossil record nor modeling of barite accumulation supports this hypothesis for the open ocean (Kelly et al. 1996; Thomas 1998; Bralower 2002; Dickens et al. 2003). The late Eocene climate changes described in the previous section are tied to an increase in upwelling and oceanic productivity (Thomas and Gooday 1996; Diester-Haass and Zahn 2001). Global productivity was low until the earliest Oligocene, when an abrupt $\delta^{13}C$ excursion, signaling a two- to threefold increase in productivity, occurred (Diester-Haass and Zachos 2003). Changes in productivity seem to parallel some, but not all, of the shifts in veneroid size (Fig. 5) across this interval. The decrease in size associated with the K/T recovery coincides with the decline in productivity, although the former actually begins before and continues long after the latter. If productivity actually increases in shallow marine environments across the PETM, this presents a problem for this hypothesis, as veneroid size continues to decrease at this time. The increase, then stabilization, of veneroid size across the E/O boundary matches well with changes in productivity. I am unaware of ecomorphological and evolutionary trends in other macrofossil clades that have been directly tied to primary productivity during this interval, although Smith and Jeffery (1998) suggest that a decrease in Danian echinoid size may be due to unpredictable nutrient supply across the K/T boundary. In addition, Allmon (2003) noted that filter-feeding turritellid species tend to radiate across the E/O boundary coincident with productivity increase.

Given the data currently available, none of the three hypotheses considered provide a consistent explanation for these trends in veneroid size. It is entirely likely that multiple factors are acting in concert to produce these trends and that different clades of veneroids are responding to different pressures.

Conclusions

Veneroid bivalves experience substantial extinction across the K/T boundary and minor extinction at the end of the mid-Eocene and at the end-Eocene. I found no evidence of size-selective extinction across any of these events; however, all three showed biased recovery patterns. Subgenera that originated during the K/T recovery were significantly smaller than subgenera that survived the extinction. In contrast, new taxa were actually larger than survivors across the mid-E and E/O events. Trends in veneroid size through time indicate that the K/T recovery accelerated an established trend toward decreasing size, whereas the mid-E and E/O initiated a short-lived trend toward larger size. These patterns are unlikely to be the result of sampling, preservation, or phylogenetic bias. Three alternative explanations, predation, temperature change, and changes in productivity, were considered. It is important to note that the effects of these three events are tied not to the extinctions themselves, but to the recoveries that follow.

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Literature Cited

Allmon, W. D. 2003. Boundaries, turnover, and the causes of evolutionary change: a perspective from the Cenozoic. Pp. 511–521 *in* Prothero et al. 2003.

Allmon, W. D., D. S. Jones, and N. Vaughn. 1992. Observations on the biology of *Turritella gonostoma* Valenciennes from the Gulf of California. Veliger 35:52–63.

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 280:731–734.

Anderson, L. C. 2001. Temporal and geographic size trends in Neogene Corbulidae of tropical America: using environmental sensitivity to decipher causes of morphologic trends. Palaeogeography, Palaeoclimatology, Palaeoecology 166:101–120.

Arnold, A. J., W. C. Parker, and S. P. Hansard. 1995. Aspects of the post-Cretaceous recovery of Cenozoic planktic foraminifera. Marine Micropaleontology 26:319–327.

Aubry, M. P., S. G. Lucas, and W. A. Berggren. 1998. Late Paleocene-early Eocene climatic and biotic events in the marine and terrestrial records. Columbia University Press, New York.

Bains, S., R. M. Corfield, and R. D. Norris. 1999. Mechanisms of climate warming at the end of the Paleocene. Science 285:724–727.

Bains, S., R. D. Norris, R. M. Corfield, and K. L. Faul. 2000. Termination of global warmth at the Paleocene-Eocene boundary through productivity feedback. Nature 407:171–174.

Bambach, R. K. 1999. Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere. Geobios 32:131–144.

Blackburn, T. M., and K. J. Gaston. 1994. Animal body size distributions: patterns, mechanisms and implications. Trends in Ecology and Evolution 9:471–474.

Bookstein, F. L. 1991. Morphometric tools for landmark data: geometry and biology. Cambridge University Press, New York.

Boulding, E. G. 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. Journal of Experimental Marine Biology and Ecology 76:201–223.

Bralower, T. J. 2002. Evidence for surface water oligotrophy during the late Paleocene Thermal Maximum: nannofossil assemblage data from Ocean Drilling Program Site 690, Maud Rise, Weddell Sea. Paleoceanography 17:13.1–13.13.

Budd, A. F., and K. G. Johnson. 1991. Size-related evolutionary patterns among species and subgenera in the *Strombina* group. Journal of Paleontology 65:417–434.

Canapa, A., I. Marota, F. Rollo, and E. Olmo. 1996. Phylogenetic analysis of Veneridae: comparison of molecular and palaeontological data. Journal of Molecular Evolution 43:517–522.

———. 1999. The small-subunit rRNA gene sequences of venerids and the phylogeny of Bivalvia. Journal of Molecular Evolution 48:463–468.

Clemens, W. A. 1986. Evolution of the terrestrial vertebrate fauna during the Cretaceous-Tertiary transition. Pp. 63–85 *in* D. K. Elliot, ed. Dynamics of extinction. Wiley, New York.

Coan, E., P. H. Scott, and F. R. Bernard. 2000. Bivalve seashells of western North America. Santa Barbara Museum of Natural History Monographs, Studies in Biodiversity 2:1–764.

Cox, L. R., et al. 1969. Mollusca 6, Bivalvia, Vols. 1, 2. Part N of R. C. Moore, ed. Treatise on invertebrate paleontology. Geological Society of America, New York, and University of Kansas Press, Lawrence.

D'Hondt, S. D., P. Donaghay, J. C. Zachos, D. Luttenberg, and M. Lindinger. 1998. Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction. Science 282: 276–279.

Dickens, G. R., T. Fewless, E. Thomas, and T. J. Bralower. 2003. Pp 11–23 *in* Wing et al. 2003.

Diester-Haass, L., and J. Zachos. 2003. The Eocene-Oligocene transitions in the equatorial Atlantic: paleoproductivity increase and positive $\delta^{13}C$ excursion. Pp. 397–416 *in* Prothero et al. 2003.

Diester-Haass, L., and R. Zahn. 2001. Paleoproductivity increase at the Eocene-Oligocene climatic transition: ODP/DSDP sites 763 and 592. Palaeogeography, Palaeoclimatology, Palaeoecology 172:153–170.

Dockery, D. T. 1984. Crisis events for Paleogene molluscan faunas in the southeastern United States. Mississippi Geology 5: 1–7.

———. 1986. Punctuated succession of Paleogene mollusks in the northern Gulf Coastal Plain. Palaios 1:582–589.

———. 1998. Molluscan faunas across the Paleocene/Eocene series boundary in the North American Gulf Coastal Plain. Pp. 296–322 *in* M.-P. Aubry, S. Lucas, and W. A. Berggren, eds. Late Paleocene-Early Eocene climatic and biotic events in the marine and terrestrial records. Columbia University Press, New York.

Dockery, D. T., and P. Lozouet. 2003. Molluscan faunas across the Eocene/Oligocene boundary in the North American Gulf Coastal Plain, with comparisons to those of the Eocene and Oligocene of France. Pp. 303–340 *in* Prothero et al. 2003.

Erwin, D. H. 1998. The end and the beginning: recoveries from mass extinctions. Trends in Ecology and Evolution 13:344–349.

Foote, M. 1991. Morphological and taxonomic diversity in a clade's history: the blastoid record and stochastic simulations. Contributions from the Museum of Paleontology, University of Michigan 28:101–140.

———. 1993. Discordance and concordance between morphological and taxonomic diversity. Paleobiology 19:185–204.

———. 1994. Morphological disparity in the Ordovician-Devonian crinoids and the early saturation of morphological space. Paleobiology 20:320–344.

———. 2000. Origination and extinction components of taxonomic diversity: general problems. *In* D. H. Erwin and S. L. Wing, eds. Deep time: *Paleobiology*'s perspective. Paleobiology 26(Suppl. to No. 4):74–102.

Gobbett, D. J. 1973. Permian Fusulinacea. Pp. 152–158 *in* A. Hallam, ed. Atlas of palaeobiogeography. Elsevier, Amsterdam.

Haasl, D. M., and T. A. Hansen. 1996. Timing of Latest Eocene molluscan extinction patterns in Mississippi. Palaios 11:487–494.

Håkansson, E., and E. Thomsen. 1999. Benthic extinction and recovery patterns at the K/T boundary in shallow water carbonates, Denmark. Palaeogeography, Palaeoclimatology, Palaeoecology 154:67–85.

Hallam, A. 1975. Evolutionary size increase and longevity in Jurassic bivalves and ammonites. Nature 258:493–496.

Hansen, T. A. 1987. Extinction of late Eocene to Oligocene mollusks: relationship to shelf area, temperature changes, and impact events. Palaios 2:69–75.

———. 1988. Early Tertiary radiation of marine mollusks and the long-term effect of the Cretaceous-Tertiary extinction. Paleobiology 14:37–51.

———. 1992. The patterns and causes of molluscan extinction across the Eocene/Oligocene boundary. Pp. 341–348 *in* Prothero and Berggren 1992.

Harper, C. W., Jr. 1975. Standing diversity of fossil groups in successive intervals of geologic time: a new measure. Journal of Paleontology 49:752–757.

Harries, P. J. 1993. Dynamics of survival following the Cenomanian-Turonian mass extinction event. Cretaceous Research 15:563–583.

Harte, M. 1998a. The evolution of *Mercenaria* Schumacher 1817 (Bivalvia: Veneridae). Pp. 305–315 *in* P. A. Johnston and J. W. Haggart, eds. Bivalves: an eon of evolution. University of Calgary Press, Calgary.

———. 1998b. Superfamily Veneroidea. Pp. 355–362 *in* P. L. Beesley, G. J. B. Ross, and A. Wells, eds. Mollusca: the southern synthesis. Fauna of Australia, Vol. 5. CSIRO Publishing, Melbourne.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, New York.

Heinberg, C. 1999. Lower Danian bivalves, Stevns Klint, Denmark: continuity across the K/T boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 154:87–106.

Hickman, C. S. 1980. Paleogene marine gastropods of the Keasey Formation of Oregon. Bulletin of American Paleontology 78:1–112.

———. 2003. Evidence for abrupt Eocene-Oligocene molluscan faunal changes in the Pacific Northwest. Pp. 71–87 *in* Prothero et al. 2003.

Hsü, K. J. 1986. Environmental changes in the time of biotic crisis. *In* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Dahlem Konferenzen Life Sciences Research Report 36:297–312. Springer, Berlin.

Ivany, L. C., E. A. Nesbitt, and D. R. Prothero. 2003a. The marine Eocene-Oligocene transition: a synthesis. Pp. 522–534 *in* Prothero et al. 2003.

Ivany, L. C., K. C. Lohmann, and W. P. Patterson. 2003b. Paleogene temperature history of the U.S. Gulf Coastal Plain inferred from $\delta^{18}O$ of fossil otoliths. Pp. 232–251 *in* Prothero et al. 2003.

Jablonski, D. 1996. Body size and macroevolution. Pp. 256–289 *in* D. Jablonski, D. H. Erwin, and J. H. Lipps, eds. Evolutionary paleobiology. University of Chicago Press, Chicago.

———. 1997. Body-size evolution in Cretaceous molluscs and the status of Cope's Rule. Nature 385:250–252.

———. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. Science 279:1327–1330.

Jablonski, D., and D. M. Raup. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. Science 268:389–391.

Jones, D. S., M. A. Arthur, and D. J. Allard. 1989. Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria* from Narragansett Bay Rhode Island. Marine Biology 102:225–234.

Kaljo, D. 1996. Diachronous recovery patterns in Early Silurian corals, graptolites, and acritarchs. *In* M. B. Hart, ed. Biotic recovery from mass extinction events. Geological Society of London Special Publication 102:127–134.

Katz, M. E., D. K. Pak, G. R. Dickens, and K. G. Miller. 1999. The source and fate of massive carbon input during the latest Paleocene thermal maximum. Science 286:1531–1533.

Kelley, P. H., and T. A. Hansen. 1996. Recovery of the naticid gastropod predator-prey system from the Cretaceous-Tertiary and Eocene-Oligocene extinctions. *In* M. B. Hart, ed. Biotic recovery from mass extinction events. Geological Society of London Special Publication 102:373–386.

Kelly, D. C., T. J. Bralower, J. C. Zachos, I. Premoli Silva, and E. Thomas. 1996. Rapid diversification of planktonic foraminifera in the tropical Pacific (ODP Site 865) during the late Paleocene thermal maximum. Geology 24:423–426.

Kidwell, S. M., and D. W. J. Bosence. 1991. Taphonomy and time-averaging of marine shelly faunas. Pp. 115–209 *in* P. A. Allison and D. E. G. Briggs, eds. Taphonomy: releasing the data locked in the fossil record. Plenum, New York.

LaBarbera, M. 1986. The evolution and ecology of body size. *In* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Dahlem Konferenzen, Life Sciences Research Report 36:69–98. Springer, Berlin.

Lockwood, R. 2004. The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves. Paleobiology 30:507–521.

McKinney, M. L. 1990. Trends in body-size evolution. Pp. 75–118 *in* K. J. McNamara, ed. Evolutionary trends. University of Arizona Press, Tucson.

McRoberts, C. A., and C. R. Newton. 1995. Selective extinction among end-Triassic European bivalves. Geology 23:102–104.

McRoberts, C. A., C. R. Newton, and A. Allasinaz. 1995. End-Triassic bivalve extinction: Lombardian Alps, Italy. Historical Biology 9:297–317.

Miller, A. I., and J. J. Sepkoski, Jr. 1988. Modeling bivalve diversification: the effect of interaction on a macroevolutionary system. Paleobiology 14:364–369.

Norris, R. D. 1991. Biased extinction and evolutionary trends. Paleobiology 17:388–399.

Palmer, A. R. 1992. Calcification in marine mollusks: how costly is it? Proceedings of the National Academy of Sciences USA 89:1379–1382.

Palmer, K. V. W. 1927. The Veneridae of Eastern America: Cenozoic and Recent. Palaeontologica Americana 1:209–522.

Passamonti, M., B. Mantovani, and V. Scali. 1998. Characterization of a highly repeated DNA family in Tapetinae species. Zoological Science of Japan 15:599–605.

———. 1999. Allozymic analysis of some Mediterranean Veneridae: preliminary notes of taxonomy and systematics of the family. Journal of the Marine Biological Association of the United Kingdom 79:899–906.

Prothero, D. R., and W. A. Berggren, eds. 1992. Eocene-Oligocene climatic and biotic evolution. Princeton University Press, Princeton, N.J.

Prothero, D. R., L. C. Ivany, and E. A. Nesbitt, eds. 2003. From greenhouse to icehouse: the marine Eocene-Oligocene transition. Columbia University Press, New York.

Raup, D. M. 1995. The role of extinction in evolution. Proceedings of the National Academy of Sciences USA 91:6758–6763.

Raup, D. M., and D. Jablonski. 1993. Geography of end-Cretaceous marine bivalve extinctions. Science 260:971–973.

Rice, W. M. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Roopnarine, P. D., and A. Beussink. 1999. Extinction and naticid predation of the bivalve *Chione* von Mühlfeld in the late Neogene of Florida. Palaeontologia Electronica 2:1–14.

Roopnarine, P. D., and C. M. Tang. 2001. Environmental and developmental controls of morphological diversity in a thermal spring gastropod from Coahuila, Mexico. Eos (Transactions of the American Geophysical Union) 82 (Fall Meeting Suppl.) Abstract B22D–0186.

Roy, K., and K. R. Martien. 2001. Latitudinal distribution of body size in north-eastern Pacific marine bivalves. Journal of Biogeography 28:485–493.

Roy, K., D. Jablonski, J. W. Valentine, and G. Rosenberg. 1998. Marine latitudinal diversity gradients: tests of causal hypotheses. Proceedings of the National Academy of Sciences USA 95:3699–3702.

Roy, K., D. Jablonski, and K. R. Martien. 2000. Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. Proceedings of the National Academy of Sciences USA 97:13150–13155.

Roy, K., D. Jablonski, and J. W. Valentine. 2002. Body size and invasion success in marine bivalves. Ecology Letters 5:163–167.

Russell, D. 1977. The biotic crisis at the end of the Cretaceous period. Syllogeus, National Museum of Natural Sciences Canada 12:11–23.

Ryder, G., D. Fastershy, and S. Gartner. 1996. The Cretaceous-Tertiary event and other catastrophes in Earth history. Geological Society of America Special Paper 307.

Saunders, W. B., D. M. Work, and S. V. Nikolaeva. 1999. Evolution of complexity in Paleozoic ammonoid sutures. Science 286:760–763.

Sheehan, P. M., and T. A. Hansen. 1986. Detritus feeding as a buffer to extinction at the end of the Cretaceous. Geology 14: 868–870.

Sheehan, P. M., P. J. Coorough, and D. E. Fastovsky. 1996. Biotic selectivity during the K/T and Late Ordovician extinction events. Pp. 477–489 *in* Ryder et al. 1996.

Smith, A. B., and C. H. Jeffery. 1998. Selectivity of extinction among sea urchins at the end of the Cretaceous period. Nature 392:69–71.

Smith, T. J., and K. Roy. 1999. Late Neogene extinctions and modern regional species diversity: analyses using the Pectinidae of California. Geological Society of America Abstracts with Programs 31:473.

Sohl, N. F., and C. F. Koch. 1983. Upper Cretaceous (Maestrichtian) Mollusca from the *Haustator bilira* assemblage zone in the East Gulf Coastal Plain. U.S. Geological Survey Open-File Report 83-451.

———. 1984. Upper Cretaceous (Maestrichtian) Mollusca from the *Haustator bilira* assemblage zone in the West Gulf Coastal Plain. U.S. Geological Survey Open-File Report 84-687.

———. 1987. Upper Cretaceous (Maestrichtian) Mollusca from the *Haustator bilira* assemblage zone in the Atlantic Coastal Plain with Further Data for the East Gulf. U.S. Geological Survey Open-File Report 87-194.

Staff, G. M., R. J. Stanton, Jr., E. N. Powell, and H. Cummins. 1986. Time averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. Geological Society of America Bulletin 97:428–443.

Stanley, S. M. 1973. An explanation for Cope's Rule. Evolution 27:1–26.

———. 1986. Population size, extinction, and speciation: the fission effect in Neogene Bivalvia. Paleobiology 12:89–110.

———. 1990. Delayed recovery and the spacing of major extinctions. Paleobiology 16:401–414.

Thomas, E. 1998. The Paleocene-Eocene benthic foraminiferal extinction and stable isotope anomalies. Pp. 214–243 *in* M.-P. Aubry et al. 1998.

Thomas, E., and A. J. Gooday. 1996. Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? Geology 24:355–358.

Valentine, J. W. 1989. How good was the fossil record? Clues from the California Pleistocene. Paleobiology 15:83–94.

Van Valkenburgh, B. 1994. Extinction and replacement among predatory mammals in the North American Late Eocene and Oligocene: tracking a paleoguild over twelve million years. Historical Biology 8:129–150.

Vermeij, G. J. 1987. Evolution and escalation. Princeton University Press, Princeton, N.J.

Wing, S. L., P. D. Gingerich, B. Schmitz, and E. Thomas, eds. 2003. Causes and consequences of globally warm climates in the early Paleogene. Geological Society of America Special Paper 369.

Zachos, J. C., and M. A. Arthur. 1986. Paleoceanography of the Cretaceous/Tertiary boundary event: inferences from stable isotopic and other data. Paleoceanography 1:5–26.

Zachos, J. C., L. D. Stott, and K. C. Lohmann. 1994. Evolution of early Cenozoic marine temperatures. Paleoceanography 9: 353–387.

Zachos, J., M. Pagani, L. Sloan, E. Thomas, and K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. Science 292:686–694.