The K/T event and infaunality: morphological and ecological patterns of extinction and recovery in veneroid bivalves

Rowan Lockwood

Abstract.—Although the causes of mass extinctions have been studied in detail, recoveries have received little attention until recently. In this study, I examine the influence of extinction versus recovery intervals on ecological patterns across the end-Cretaceous (K/T) event in veneroid bivalves. Systematic and stratigraphic data were collected for 140 subgenera of veneroids, ranging from the Late Cretaceous through Oligocene of North America and Europe. Morphological data were collected for 1236 specimens representing 101 subgenera. Extinction selectivity and differential recovery were assessed with respect to morphology, and by extension, burrowing ecology in these bivalves. Eighty-one percent of veneroid subgenera went extinct at the K/T and diversity did not return to preextinction levels until 12 million years later. Despite the severity of the K/T extinction, I found little evidence of morphological or ecological selectivity. The K/T recovery, in contrast, was strongly biased toward taxa with deep pallial sinuses (i.e., toward deeper burrowers). For veneroids, the morphological and ecological effects of the K/T event are not tied to the extinction itself, but to the recovery that followed. The K/T recovery initiated a trend toward deeper burrowing that helped to establish veneroids as one of the most abundant and successful groups of modern marine bivalves.

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Introduction

To understand the role that mass extinctions play in shaping morphological and ecological patterns, it is important to examine both the extinctions themselves and the recovery intervals that follow. Similar to extinctions, recoveries can influence the ecology and evolutionary history of a biota. Although the causes and immediate consequences of mass extinctions have been studied in detail, recoveries have received little attention until recently (Erwin 1996, 1998a,b, see papers in Erwin 1999, 2001; see papers in Hart 1996; Kirchner and Weil 2000).

Recent studies of recovery in the fossil record have involved the collection of high-resolution community composition data from the first one to two million years after an event (e.g., Harries 1993; see papers in Hart 1996; Håkansson and Thomsen 1999; Heinberg 1999; Twitchett 1999; Wood 2000). Available data suggest that the amount of time required for diversity to return to pre-extinction levels (ranging from 250 Kyr to 20 Myr) differs in different clades crossing the same extinction boundary, and in the same clade crossing different extinction boundaries (see for example Copper 1994a,b; Arnold et al. 1995; Erwin 1996; see papers in Hart 1996; Retallack et al. 1996; Smith et al. 1999; Arens and Jahren 2000). Although the need for a more comprehensive understanding of recovery is recognized, few studies have used the data available to address large-scale ecological or evolutionary questions.

The goal of this study is to examine ecomorphological patterns of extinction and recovery across the end-Cretaceous (K/T) event in veneroid bivalves. The majority of veneroids are infaunal suspension-feeding bivalves that are abundant and extremely successful in modern shallow-marine environments. Although they originated in the Devonian, these bivalves were a minor constituent of shelf habitats until the early Cenozoic, when they diversified rapidly and radiated into deeper burrowing niches (Palmer 1927; Cox et al. 1969; Harte 1998a,b, 1999). This shift in ecological dominance and diversity after the K/T mass extinction, in addition to the fact that these bivalves are well pre-

served and abundant in a variety of paleoenvironments, makes the veneroids an ideal clade in which to study the relative influence of extinction versus recovery intervals on ecomorphological patterns.

The evolutionary impact of an extinction event involves not only the number of taxa lost, but also the elimination and subsequent exploration of areas of morpho- and ecospace. In this study, the consequences of the K/T event are examined, not only from the standpoint of taxonomic diversity, but also with respect to the morphology and ecology of veneroids. The close connection between shell morphology and burrowing in these bivalves makes this examination possible. Several authors (for example Stanley 1970, 1979; Kondo 1987) have qualitatively or quantitatively described the relationship between pallial sinus shape and burrowing depth in veneroids. As pallial sinus depth increases, burrowing depth also increases. This ecomorphological relationship will be used to document the impact of the K/T extinction on the early Cenozoic history of veneroid bivalves.

Methods

This study focuses on the late Mesozoic and early Cenozoic evolutionary history of three closely related (Cox et al. 1969; Abbott 1974; Harte 1998a,b; Slack-Smith 1998a,b; Abbott and Dance 2000) superfamilies of heterodont bivalves: the Veneroidea, Arcticoidea, and Glossoidea. For the sake of simplicity, these superfamilies are collectively referred to here as veneroids. Systematic data were collected for 719 species and 140 subgenera of veneroids from the Late Cretaceous through Oligocene of 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. Identification of tropical regions was based on the geographic occurrences of large foraminifera in the Late Cretaceous, Paleocene, and Eocene (Dilley 1977; Hottinger 1977).

Taxonomic identifications were based on personal observation and alpha-taxonomic information available in the literature (including Dall 1902; Jukes-Browne 1908; Stephenson 1923, 1941, 1952, 1954, 1955; Marwick 1927; Palmer 1927; Frizzell 1936; Tremlett 1953; Palmer and Brann 1965; Moore 1969; Dockery 1977, 1982; Vokes 1980; Sohl and Koch 1983, 1984, 1987; Dhondt 1987; Saul and Popenoe 1992; Saul 1993; Kirby and Saul 1995; Roopnarine 1996; Harte 1998a,b; Roopnarine and Vermeij 2000, among others). A subgeneric taxonomy is available online at http://dx.doi.org/10.1666/02055.s1.

Stratigraphic occurrences were compiled for 140 veneroid subgenera from museum collections, fieldwork, and the literature. First and last appearance data (FAD and LAD, respectively) were established for each subgenus on the basis of global occurrence data. Stratigraphic range data for subgenera are available online in the Supplementary Online Material repository. 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 tallying taxa that cross boundaries (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 (see Foote 2000).

Morphological data were collected from 1236 museum and field-collected specimens representing 101 subgenera from the Late Cretaceous through Oligocene of North America and Europe. Specimens were photographed in standard orientation and shell shape was quantified in two orientations, lateral and cross-sectional (Fig. 1), by using 100 equally spaced points distributed around each outline. Pallial line shape was also quantified by using 100 equally spaced points distributed around the pallial line, stretching from its intersection with the anterior adductor muscle scar to its intersection with the posterior adductor muscle scar. Images were recorded with a Sony Hi-8 video camera with a macro
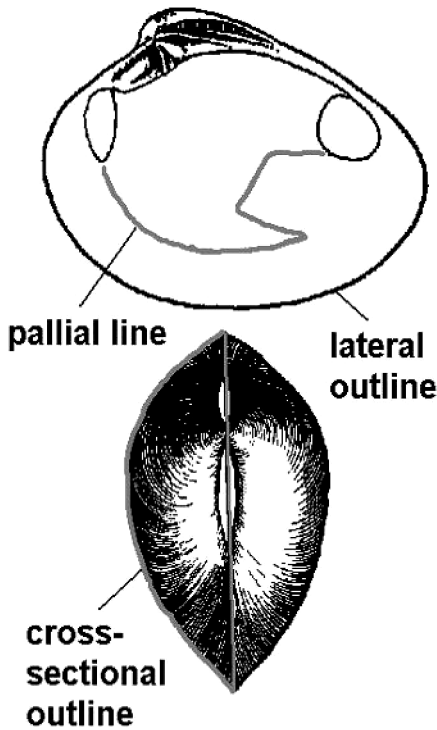
FIGURE 1. Morphological measures. One hundred equally spaced points were digitized around the lateral shell outline, cross-sectional shell outline, and pallial line.

lens and a Sony digital video camera. Optical digitization was performed with Optimas 5.2 for Windows.

Elliptical Fourier analysis (EFA) was used to summarize variation in shell and pallial line shape (Ferson et al. 1985; Rohlf and Ferson 1992; Crampton 1995). Specimens were standardized according to size by calculating the area of the enclosed outline and dividing coordinates by the square root of this area (Rohlf and Ferson 1992). Invariance to location was achieved by estimating the centroid coordinates for the enclosed region and subtracting these from the original coordinates (Rohlf and Ferson 1992). EFA was applied separately to the lateral (Lateral) outlines, cross-sectional (X-Sectional) outlines, and the closed shape of the pallial (Pallial) outlines of 1182, 1094, and 559 specimens, respectively. Principal components analysis (PCA) was then applied to the variance-covariance matrices of the lateral, cross-sectional, and pallial harmonics separately. PCA axes that summarized 99% of the original variation were retained and scores were interpreted by plotting sample outlines along each axis. The scores from these axes are referred to as PCA measures of morphology. A simple measure of pallial sinus perimeter was also derived by standardizing the pallial line data according to size and rotation and measuring distance (PD) around the pallial line. Taxa with larger pallial sinuses recorded higher values of PD. Multivariate analyses were performed with Statistica 5.0 and EFA (Rohlf and Ferson 1992) for Windows.

EFA has been criticized recently on two counts (Haines and Crampton 2000): (1) that the method produces a relatively large number of Fourier descriptors that are not computationally independent of each other and (2) that the method downweights all harmonics above the first, effectively ignoring high-frequency information. Neither of these criticisms poses a substantial problem for the application of EFA in this study. The problem of redundancy is minimized by the use of PCA to summarize shape change. Downweighting is not a major concern because the number of harmonics was selected specifically to ensure that sufficient shape detail was retained. Finally, the results of this study do not vary substantially, regardless of whether shell and pallial shape is quantified with EFA, eigenshape analysis (Lohmann 1983; MacLeod 1999), relative warps analysis (Bookstein 1991; Dryden and Mardia 1998), or PCA on raw (x, y) coordinates. The robustness of these results to a variety of morphometric methods makes it unlikely that Haines and Crampton's (2000) criticisms pose a significant problem for this study.

Global stratigraphic ranges were used to categorize subgenera as victims (extinct at the K/T), survivors (survived the K/T), or new taxa (originated during the recovery interval). Recovery was defined as the interval required for veneroid diversity to reach preextinction levels. Extinction selectivity was assessed by comparing the means of victims and survivors, whereas differential, or biased, recovery was assessed by comparing the means of survivors and new taxa. Extinction selectivity and differential recovery were examined for both the simple (PD) measures and for the
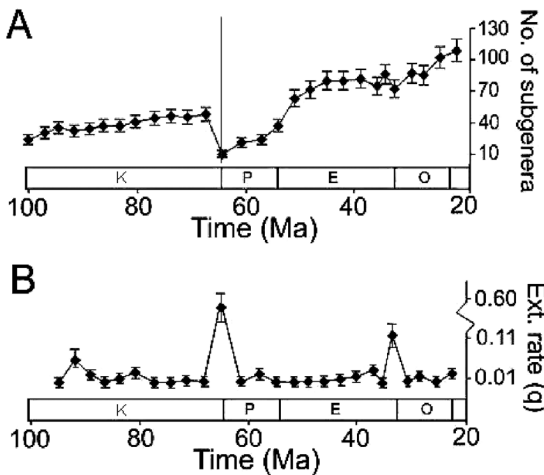
A

B

FIGURE 2. Taxonomic diversity patterns in veneroids. A, Global subgeneric diversity measured as the number of taxa crossing boundary intervals. Error bars are approximate and represent the square root of the number of taxa crossing each boundary (Foote 1993). 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).

PCA morphological measures (i.e., the axes retained from the lateral, cross-sectional, and pallial PCA analyses). All of the specimens representing a subgenus throughout its stratigraphic (Late Cretaceous through Oligocene) and geographic (in North America and Europe) range were pooled in order to calculate the mean of each morphological character for each subgenus. Kolmogorov-Smirnov one-sample tests of normality revealed no significant deviation from a normal distribution for any of the morphological measures after adjustment for multiple comparisons (all $D_{88} >$ 0.14, $p > 0.05$). Subsequent analyses of these measures were performed with parametric statistics.

Sequential Bonferroni adjustment was applied to each independent pool of statistical analyses, defined as a group of analyses using the same morphometric data (i.e., lateral, cross-sectional, or pallial outline) and statistical techniques. Sequential Bonferroni was chosen over standard Bonferroni because it represents a more powerful approach and is
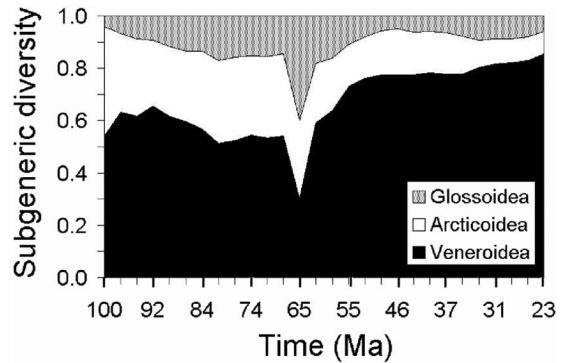

FIGURE 3. Plot of proportional subgeneric diversity for the three superfamilies examined in this study: Glossoidea, Arcticoidea, and Veneroidea.

more likely to retain significant differences between populations (Rice 1989).

Results

Taxonomic Diversity Patterns

Like most marine invertebrates, veneroids underwent a substantial extinction at the K/T boundary. Overall subgeneric diversity dropped by 79% (Fig. 2A). When extinction rate is plotted from the Late Cretaceous through Oligocene (Fig. 2B), it is evident that the K/T represented an unusually severe event for veneroids. The recovery after the K/T was rapid, although subgeneric diversity did not reach preextinction levels until approximately 53 Ma (i.e., 12 Myr after the extinction event). After the K/T, the veneroids continued to diversify at a slightly accelerated rate until the end of the middle Eocene.

When the proportional diversity of subgenera representing each of the three superfamilies is plotted (Fig. 3), it is clear that the proportional diversity of the Veneroidea increased during the K/T recovery, while the proportional diversity of the Arcticoidea and Glossoidea decreased. Diversity in the three superfamilies was split equally following the extinction, but the Veneroidea (which have been historically more diverse than the Arcticoidea and Glossoidea since the Cenomanian) diversified more quickly than the other two superfamilies during the recovery.

Veneroid Morphospace

The PCA of lateral shell outline produced six axes that accounted for 99% of the original
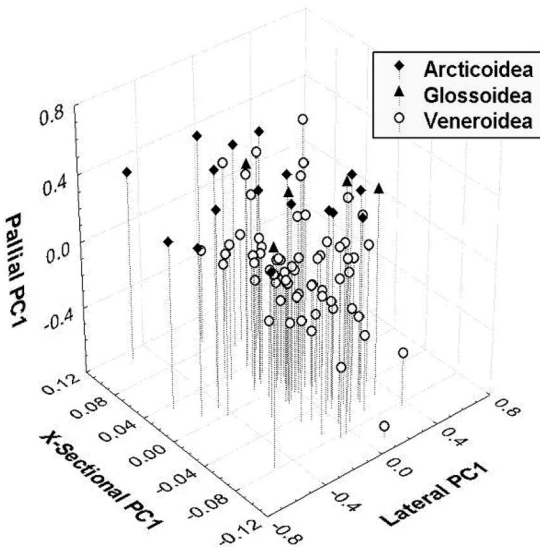
FIGURE 4. Three-dimensional morphospace constructed from the first principal component axes from the lateral shell (Lateral PC1), cross-sectional shell (X-Sectional PC1), and pallial line (Pallial PC1) analyses. Points represent subgenera and are categorized according to superfamily. Subgenera with deeper pallial sinuses are distributed in the lower part of the plot.

shape variation and summarized changes in overall shell shape, ellipticity, and position of the umbo in the anterior-posterior plane. The PCA of cross-sectional shell outline produced ten axes that accounted for 99% of the original variation and described changes in globosity, the position of maximum width, and general shell shape. Finally, the PCA of pallial line shape produced nine axes that accounted for 99% of the original shape variation and summarized changes in pallial sinus depth, shape, and angle. The scores from each of these 25 axes were used in subsequent selectivity analyses to represent PCA measures of morphology. The PCA measures of pallial sinus morphology correlated strongly with the simple measure (Pallial PC1 vs. PD: $r_{559} = 0.95$).

To examine the distribution of taxa in morphospace, the first principal component axes for the lateral shell (Lateral PC1, which accounts for 86% of the original shape variation), cross-sectional shell (X-Sectional PC1, which accounts for 45% of the original shape variation), and pallial line (Pallial PC1, which accounts for 62% of the original shape variation) analyses were plotted against each other in three-dimensional space (Fig. 4). Lateral

PC1 describes differences in general shell shape, with rectangular subgenera such as *Coralliophaga* s.s. and *Neotrapezium* displaying low values, circular genera such as *Dosinia* and *Cyprimeria* displaying mid-range values, and triangular subgenera such as *Tivela* s.s. and *Transennella* displaying high values. Posterior PC1 summarizes differences in cross-sectional shell shape. Subgenera with round cross-sectional shapes, such as *Mercenaria* and *Omnivenus*, have low values, whereas subgenera with somewhat squarer cross-sectional shapes, such as *Petricola* and *Eomiodon*, display high values. Pallial PC1 describes differences in pallial sinus depth. Taxa with deep pallial sinuses including *Grateloupia* s.s. and *Dosinia* s.s. have low values, taxa with shallow pallial sinuses such as *Lirophora* have middle values, and taxa with no pallial sinus including *Arctica* have high values. When subgenera are plotted in morphospace according to superfamily (Fig. 4), it is clear that subgenera within the superfamily Arcticoidea tend to have high Pallial PC1, variable Lateral PC1, and mid-range to high X-Sectional PC1 values, and lack pallial sinuses. Subgenera within the superfamily Glossoidea all have high Pallial PC1, mid-range Lateral PC1, and mid-range to low X-Sectional PC1 values, and also lack pallial sinuses. Subgenera within the superfamily Veneroidea tend to have low Pallial PC1, mid-range Lateral PC1, and variable X-Sectional PC1 values and display a range of pallial sinus depths. Of the three axes plotted here, Pallial PC1 is the most effective at differentiating these three superfamilies. For example, the Glossoidea and Arcticoidea plot toward the top of the morphospace, whereas the Veneroidea plot toward the bottom. The relationship between morphology and burrowing behavior in veneroids predicts that deep-burrowing taxa (i.e., taxa with deeper pallial sinuses) are distributed throughout the lower half of this plot.

Patterns of K/T Extinction and Recovery

Extinction Selectivity and Differential Recovery.—To test for K/T selectivity, differences between victims, survivors, and new taxa were examined for each of the 26 simple and PCA morphological measures. The extinction
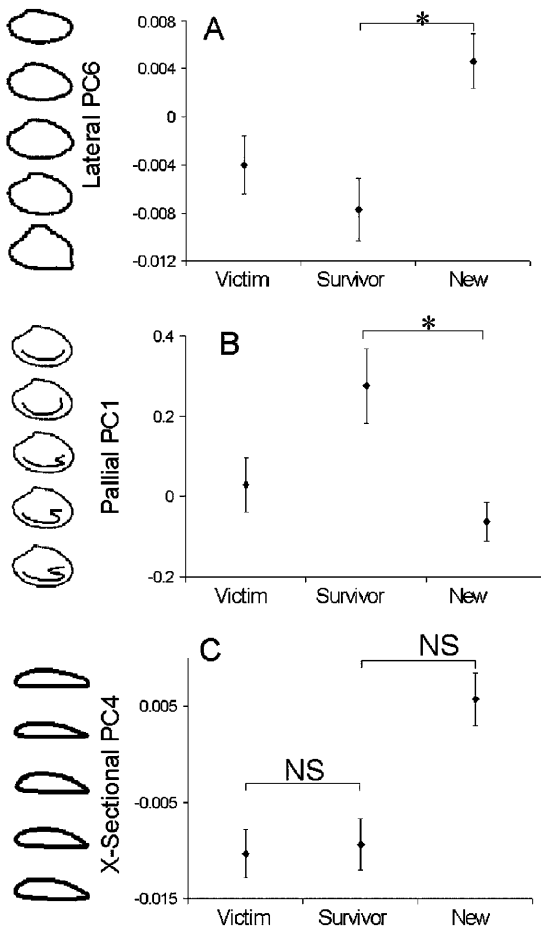
FIGURE 5. Mean (±SE) of three PCA measures of morphology, comparing K/T victims, survivors, and new taxa. A, Lateral PC6. No significant difference was recorded between victims and survivors ($t_{19,9} = 0.93$, $p > 0.05$) after Bonferroni correction. Survivors have significantly lower values of Lateral PC6 than new taxa ($t_{9,29} = -2.83$, $p = 0.04$) after Bonferroni correction. B, Pallial PC1. No significant difference was recorded between victims and survivors ($t_{15,8} = -2.14$, $p > 0.05$) after adjustment for multiple comparisons. Survivors have significantly higher values of Pallial PC1 than new taxa ($t_{8,28} = 3.31$, $p = 0.02$) even after adjustment for multiple comparisons. C, X-Sectional PC4. No significant difference was recorded between victims and survivors ($t_{19,9} = -0.23$, $p > 0.05$) after Bonferroni correction. No significant difference was recorded between survivors and new taxa ($t_{9,29} = -2.96$, $p = 0.06$) after Bonferroni correction.

was not selective with respect to any of these measures, after adjusting for multiple comparisons. In contrast, the recovery was significantly biased, even after Bonferroni correction. Survivors have significantly lower values of Lateral PC6 ($t_{9,29} = -2.83$, $p = 0.04$) and higher values of Pallial PC1 ($t_{8,28} = 3.31$, $p =$
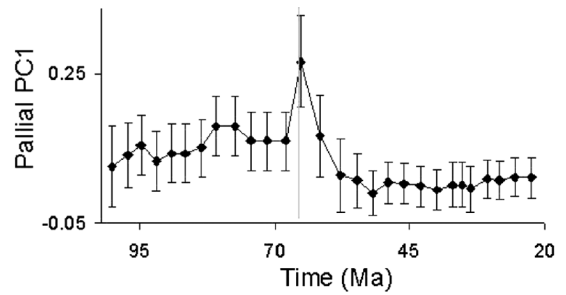

FIGURE 6. Burrowing depth of veneroids through time. Mean (±SE) of Pallial PC1 from the Late Cretaceous to early Cenozoic.

0.02) than new taxa (Fig. 5A,B). The outlines plotted on Figure 5A,B highlight the changes in shell and pallial shape summarized by these two axes. Surviving taxa have significantly less elliptical shells and shallower pallial sinuses than new taxa (Fig. 5A,B). Given the relationship between pallial sinus shape and burrowing behavior in veneroids, these results indicate that the recovery was biased toward deeper-burrowing taxa. The PCA measures of cross-sectional shape showed no significant difference between survivors and new taxa, although there is a nonsignificant (after Bonferroni adjustment) tendency for survivors to have lower values of X-Sectional PC4, and hence more globose shells, than new taxa ($t_{9,29} = -2.96$, $p = 0.06$; Fig. 5C). It is also satisfying to note that the results for the simple morphological measure of pallial sinus size (PD) agree with the PCA measures. Survivors have significantly lower values of PD (i.e., shorter pallial lines and hence smaller pallial sinuses) than new taxa ($t_{8,28} = -3.18$, $p = 0.03$). S. M. Stanley (personal communication 2003) has argued that pallial sinus depth is not as accurate a proxy of burrowing depth as pallial sinus area, but that the square root of pallial sinus depth can be used as a substitute for pallial sinus area. Use of the square root of pallial sinus depth (Pallial PC1) as a proxy for pallial sinus area produced identical results to those outlined above.

Pallial PC1 was used to examine mean (±SE) burrowing depth in veneroids from the Late Cretaceous to the early Cenozoic (Fig. 6). Burrowing depth decreased slightly throughout the Late Cretaceous, with a massive decrease observed across the K/T boundary.
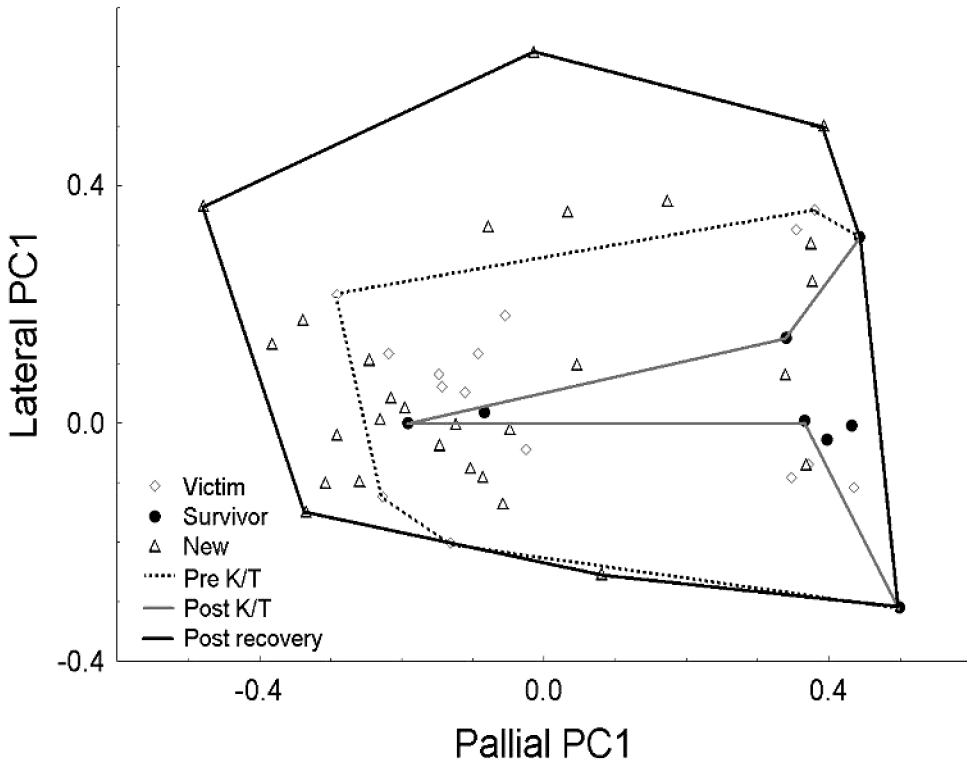
FIGURE 7. Extinction selectivity and differential recovery of subgenera along Pallial PC1 and Lateral PC1. This plot makes it possible to compare morphospace occupation immediately before the K/T extinction (pre K/T), immediately after the K/T extinction (post K/T), and immediately after the K/T recovery (post recovery). The points represent subgenera categorized on the basis of whether they are K/T victims, survivors, or new taxa. The outlines represent the entire range of victims, survivors, and new taxa.

This decrease was reversed during the K/T recovery, which involved a marked shift to deeper burrowing niches, where veneroids have remained unchanged for the rest of the early Cenozoic. It should be noted that veneroids inhabit deeper niches after the K/T recovery than before the extinction and that this shift to deeper niches appears to coincide with rapid diversification.

Morphospace Occupation.—Pallial PC1 and Lateral PC1 (Fig. 7) were used to plot the morphological range of veneroids before the K/T extinction (pre K/T; includes both victims and survivors), immediately after the K/T extinction (post K/T; includes survivors), and immediately after the K/T recovery (post recovery; includes both survivors and new taxa). This plot highlights the contraction and subsequent expansion of morphological range during the extinction and recovery. Although the extinction was not significantly selective in

morphospace, this plot indicates that taxa on the left side of the space, in particular the upper and lower areas, were lost preferentially. The taxa originating during the recovery did not simply refill the areas of morphospace lost, but expanded outward, along the upper and left side of the plot. It is interesting to note that the outer boundaries of the post-recovery morphospace are defined almost entirely by representatives of the superfamily Veneroidea. The rapid taxonomic diversification of this particular superfamily after the K/T (Fig. 3) coincided with marked morphological diversification and the exploration of novel morphologies.

To examine the refilling of veneroid morphospace after the K/T in more detail, the progression of the recovery was plotted chronologically across morphospace (Fig. 8). The recovery was divided into three intervals approximately 4 Myr in duration (65–61.3, 61.2–
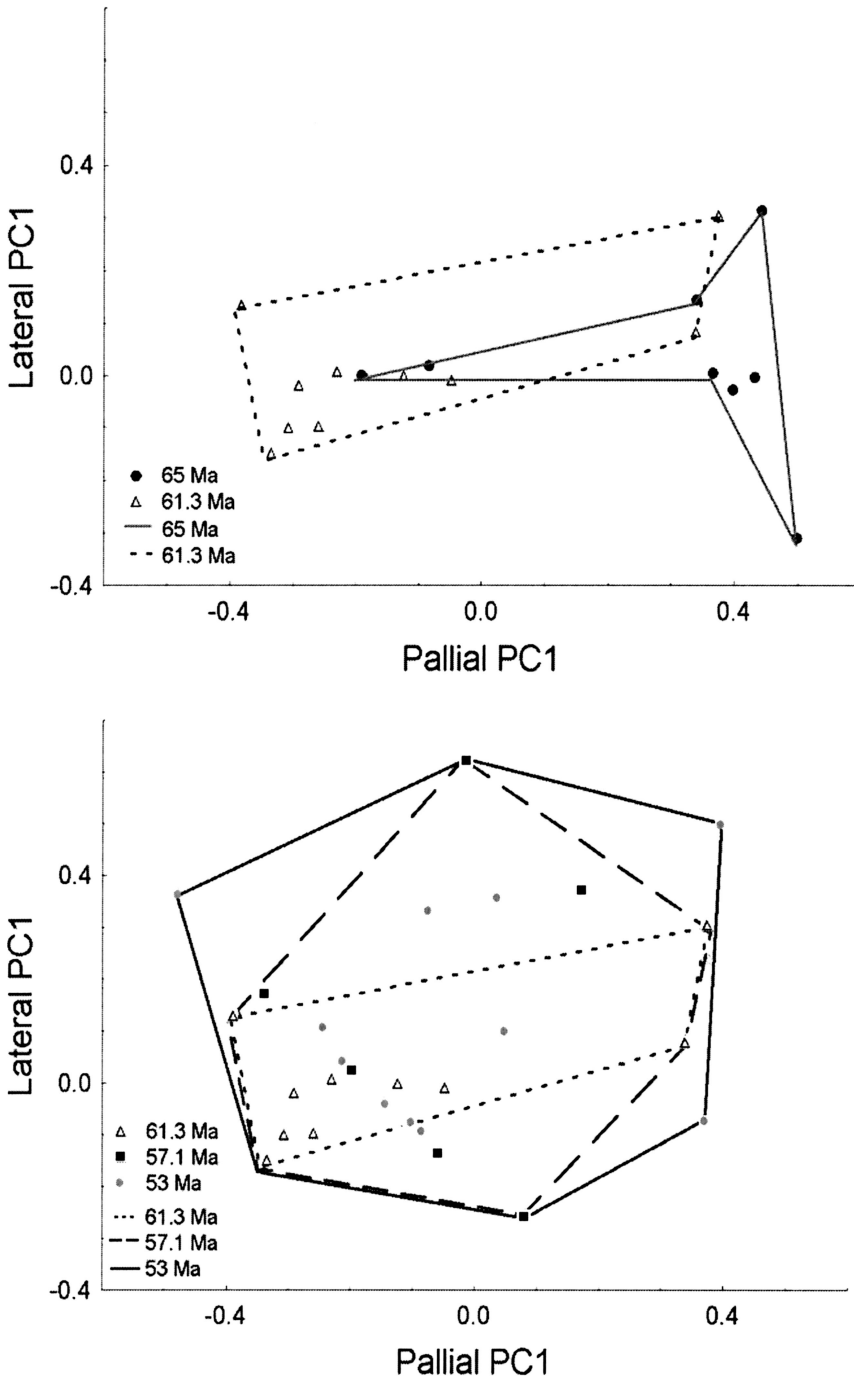
FIGURE 8. Refilling of morphospace during the K/T recovery. Top, Points represent the K/T survivors (65 Ma) and taxa that originated during the first interval of the recovery (61.3 Ma). Outlines represent the entire range of survivors (65 Ma) and taxa that originated during the first interval of the recovery (61.3 Ma). Bottom, Points represent the taxa that originated during the first (61.3 Ma), second (57.1 Ma), and third (53 Ma) intervals of the recovery. The outlines represent the cumulative range of taxa that originated in each successive interval of the recovery (i.e., the outline for 57.1 Ma includes taxa that originated in the first and second interval of the recovery).

57.3, 57.2–53Ma) and the cumulative range of morphospace in each of these intervals was plotted in turn. The recovery was characterized by (1) exploration and infilling of novel morphospace associated with deeper pallial sinuses and (2) expansion into novel morphospace associated with slightly more triangular lateral outlines. The exploration of novel pallial morphospace occurs primarily during the first interval of recovery (Fig. 8, top), although one subgenus from the final interval also contributes to the pattern. The taxa originating during the first interval lie slightly above and to the left of the taxa that survived the extinction, indicating that the former have deeper pallial sinuses than the latter (Fig. 8, top). During the second interval of recovery (Fig. 8, bottom), originating taxa spread to the upper and lower portions of the plot, but do not expand laterally. These taxa are partially responsible for the expansion into novel lateral morphospace (although two subgenera from the final interval also contribute to the pattern), but are merely filling in the new areas of pallial morphospace established during the first interval. During the third and final interval, originating taxa continue to expand toward the top and, in the case of one subgenus, the left (indicating deeper pallial sinuses) sides of the plot.

Discussion

Extinction Selectivity at the K/T

Our understanding of mass extinction selectivity is still growing, but much of what we do know is based on patterns associated with the K/T. Most of these studies have yielded little evidence for selectivity, although K/T survivors tend to be geographically widespread, and in some clades, they tend to have planktonic life cycles (diatoms [Kitchell et al. 1986]), small body sizes (birds [Clemens 1986]; terrestrial vertebrates [Russell 1977]), and deposit feeding lifestyles (aporrhaid gastropods [Roy 1994]; echinoids [Smith and Jeffery 1998; but see Jablonski and Raup 1995; Heinberg 1999]). Morphological selectivity across the K/T extinction has been documented in planktonic foraminifera (Norris 1991, 1992), biconvex brachiopods (McGhee 1995), and ho-

lasteroid echinoids (Eble 2000), but it is unclear whether these morphological patterns are independent of geographic or bathymetric range.

I found no evidence for extinction selectivity across the K/T according to morphology, and by extension, burrowing ecology in veneroids.

Extinction and Recovery in Morphospace

Patterns of K/T extinction and recovery in morphospace (Fig. 8) indicate that the recovery proceeded in a step-by-step fashion, starting from the area of morphospace immediately above the area occupied by the survivors and diffusing outward. Novel areas of pallial morphospace were explored during the first interval of recovery (65–61.3 Ma), filled in during the second interval (61.2–57.3 Ma), and enlarged slightly during the final interval (57.2–53 Ma). Expansion and limited infilling of novel lateral morphospace occured throughout both the second and third intervals of recovery. The morphospace occupation of the subgenera originating during the first interval somewhat mirrors the distribution of the survivors (Fig. 8, top), but this similarity is lost as veneroids continue to diversify morphologically throughout the duration of the recovery (Fig. 8, bottom). Although the extinction selectivity documented in this morphospace is not statistically significant, it may be sizable enough to affect the distribution of taxa originating during the initial stages of recovery.

Biased Origination of Deep Burrowers after the K/T

Possible Explanations for Increased Infaunality. Given the relationship between morphology and burrowing behavior in veneroids, these patterns indicate that the K/T recovery favored deeper-burrowing taxa. A variety of possible explanations for this pattern must be considered, including sampling, preservational bias, taxon sorting, predation pressure, and the refilling of ecological niches. It is unlikely that either sampling or preservation could artificially produce this increase in veneroid burrowing depth. Shallow and deeply burrowing veneroids inhabit a variety of paleoen-

vironments and there is no a priori reason to suppose that shallow-burrowing taxa are more likely to be sampled than deep-burrowing taxa (or vice versa). I quantified the relationship between sampling (measured by using the number of localities sampled in this study as a proxy) and the simple measure of pallial sinus depth (PD) by plotting first-order differences of sampling versus first-order differences of PD. First-order differences (i.e., the difference between a measure at one time interval [t] and that same measure at the next interval [t + 1]) help to minimize the problem of autocorrelation in temporal sequence data. Temporal patterns of sampling and sinus depth are not correlated ($r_{26} = 0.01$, $p = 0.98$), indicating that sampling is not significantly influencing these results.

Preservation is also unlikely to yield this pattern. Although deeper-burrowing bivalves are more likely to be preserved than shallow burrowers, the absolute range of veneroid burrowing depths is limited and is unlikely to produce a systematic bias in preservation. Even if preservation was affected by burrowing depth, one would expect that, as preservation improves throughout the early Cenozoic, this would produce an increase in the number of shallow burrowers. Burrowing depth in veneroids does not vary significantly after the K/T recovery, despite improved preservation.

Taxonomic Sorting?—Another explanation for this pattern involves taxonomic sorting among the three superfamilies examined. Because the proportional diversity of the superfamily Veneroidea increased throughout the recovery, while the proportional diversity of the Arcticoidea and Glossoidea decreased, it is possible that this pattern is due simply to the differential radiation of the Veneroidea, which exhibit a much greater range of burrowing depths than the other two superfamilies. To examine this possibility, differential recovery was examined within the superfamily Veneroidea alone. Although sinus depth ($t_{3,25} = -0.78$, $p > 0.10$) showed no significant difference between survivors and new taxa within this superfamily (in part because of the limited sample size of veneroid survivors, $n = 4$), there was a tendency for survivors to have

shallower pallial sinuses. The trends are in the same direction as those observed for the Veneroidea, Glossoidea, and Arcticoidea as a whole. Although these results indicate that taxonomic sorting may have played a role in the shift toward deeper burrowing in veneroids, the fact that this pattern can also be differentiated, albeit weakly, within the superfamily Veneroidea, indicates that other factors (such as predation or ecological refilling) may be at work here.

It is also important to examine whether taxonomic sorting at lower taxonomic levels is responsible for this shift into deeper burrowing niches. Could a single lineage radiating successfully, for reasons unrelated to infaunality, produce this pattern? Thorough exploration of this question requires a well-resolved phylogeny; however, phylogenetic analysis of major subfamilies within the fossil Veneroidea has never been attempted. Given the hundreds of subgenera and thousands of species this superfamily comprises, such an analysis was beyond the scope of this work. Theoretical modeling by Sepkoski and Kendrick (1993; see also Robeck et al. 2000) suggests that traditional paleontological genera can adequately capture lineage information in studies of mass extinction. Therefore, as a preliminary approach to this problem, I examined patterns within the Veneroidea according to subfamily designations both established in the systematic literature (see for example Cox et al. 1969; Dockery 1977, 1982; Vokes 1980; Harte 1998a,b, 1999) and revised for each subgenus individually. The recovery involved the origination of taxa from two families (out of the two Veneroidea families occurring in the Mesozoic and early Cenozoic) and nine subfamilies (out of the ten Veneridae subfamilies occurring in the Mesozoic and early Cenozoic). The trend toward deeper burrowing (as assessed via Pallial PC1 values) was produced by representatives from a diverse array of subfamilies (Meretricinae, Dosiniinae, Pitarinae, Tapetinae, Clementiinae, and Gemminae) within the Veneridae. The fact that such a diversity of subfamilies contributed to this pattern suggests that taxonomic sorting is not operating strongly at lower taxonomic levels. It is worth noting, however, that subgenera within the

subfamilies Pitarinae and Meretricinae are diversifying particularly rapidly throughout this interval and are contributing disproportionately to this pattern. It is difficult to pinpoint any evolutionary innovations that distinguish these two subfamilies, as they are characterized by the typical life habits, feeding modes, physiology, and ecology that define the Veneridae in general.

Increased Predation Pressure?—An increase in predation pressure immediately after the K/T extinction may also explain this result. Hansen (1988) and Hansen et al. (1987, 1993) tracked ecological patterns during the K/T recovery in Gulf Coastal Plain molluscs and noted a very slight decrease in the number of nonsiphonate versus siphonate suspension-feeding molluscs (see, for example, Hansen et al. 1987: Fig. 5). This pattern was documented for both bivalves and gastropods and continued from the mid to late Paleocene until the early Eocene. Hansen (1988) and Hansen et al. (1987, 1993) attributed this pattern to a possible link between the radiation of predatory gastropods and the decreased prevalence of shallow burrowers, suggesting a continuation of the general diversification of marine predators referred to as the Mesozoic Marine Revolution (Vermeij 1977). To explore the possibility that predation drove this modest shift toward deeper burrowing, Kelley and Hansen (1996) compiled data on naticid drill-hole frequencies in bivalves and gastropods from the Late Cretaceous through Oligocene of the North American Coastal Plain. They documented a substantial increase in drilling frequency immediately after the K/T (and the end-Eocene; see also Kelley and Hansen 1993) and suggested that this pattern may result from cyclic escalation of the naticid predator-prey system. In the Kelley and Hansen (1993) scenario of cyclic escalation, mass extinctions are thought to perturb the system, causing drilling frequencies (i.e., predation attempts) to increase until prey species develop antipredatory adaptations, such as increased shell thickness, increased burrowing depth, or increased shell ornament (Kelley and Hansen 1996).

But how do mass extinctions perturb these systems in the first place? Vermeij (1987) has suggested that highly ''escalated'' species (i.e., species with antipredatory adaptations) should be selected against during mass extinction events (particularly those involving cooling or a decline in primary productivity) because of the energetic costs associated with these adaptations. Vermeij's (1987, 1994) hypothesis predicts that the incidence of antipredatory adaptations should be low immediately following an extinction event and should increase rapidly (as a result of selective pressure to avoid predation) throughout the recovery interval. Hansen et al. (1999) tested the possibility that highly ''escalated'' species are preferentially removed during mass extinction by examining extinction selectivity at the K/T (and a series of Cenozoic extinctions) with respect to antipredatory adaptations (i.e., shell thickness, ornament). They found no evidence for selective extinction of ''escalated'' taxa (Hansen et al. 1999). This result agrees well with my findings for K/T veneroids. Similar to Hansen et al.'s (1999) study, I found no significant extinction selectivity against highly ''escalated'' taxa, in this case, deeper burrowers.

Two other studies touch, albeit tangentially, on the role that infaunality plays during the K/T recovery. Heinberg (1999) recognized a sharp increase in the diversity of infaunal relative to epifaunal bivalves in the lower Danian of Denmark, but he attributed this pattern to an absence of bryozoans, which act as substrate for epifaunal bivalves. He also maintained that the increase in infaunality is not significantly greater than the lateral variations in infaunality (from habitat to habitat) observed in Danish localities before the K/T (Heinberg 1999). Jablonski (1998) tracked the recovery of species diversity after the K/T for non-siphonate bivalves and muricoid gastropods in four geographic regions. Non-siphonate bivalves (i.e., shallow infaunal taxa) represented a smaller proportion of overall bivalve species after the K/T than they did before the K/T, but only in the Gulf Coast of North America and in North Africa. These bivalves actually appeared to increase proportionally after the K/T in Northern Europe and Pakistan (Jablonski 1998). Muricoid gastropods, which are one of the most diverse clades

of predatory gastropods (and are known to prey on veneroids) showed similarly heterogeneous results. Muricoids increased in proportional diversity after the K/T, but only in the Gulf Coast of North America and in Pakistan.

The patterns described above suggest one possible hypothesis for the increase in depth of veneroid burrowing during the K/T recovery. Infaunality is thought to be an important antipredatory adaptation in bivalves in general (Vermeij 1977, 1994), and it is possible that veneroids showed increased infaunality after the K/T in response to increased rates of predation.

Refilling of Ecological Niches?—A final possible explanation for the differential recovery of deeper-burrowing veneroids after the K/T relates to the pattern of extinction and the refilling of empty ecological niches. K/T victims tend to have deeper pallial sinuses than survivors, although this pattern is not statistically significant after adjusting for multiple comparisons (Fig. 5A). It is possible that the removal of veneroids from this area of morpho- and ecospace spurred an immediate refilling of infaunal niches as soon as environmental conditions stabilized. If the shift in burrowing depth represented an immediate refilling of infaunal niches, one might expect pallial sinus depth to increase in the first few million years of the recovery, then stabilize subsequently. This possibility can be examined by tracking the mean ($\pm$SE) of Pallial PC1 throughout the course of the K/T recovery (Fig. 6). This plot indicates that both the mean and overall range of this measure shifted throughout this interval and that the shift lasted from 65 to 57.1 Ma. This pattern suggests strong selection for deeper burrowing in the first two-thirds of the recovery, weakening by the end of the recovery. Unfortunately, this is also the pattern that one would expect if increased predation were driving veneroids deeper, but only in the initial stages of the recovery. To assess this scenario properly, a variety of proxies for predation pressure (including for example, shell thickness, ornament, and gastropod drilling) need to be examined during the initial stages of the recovery, with extremely fine-scale stratigraphic resolution. Unfortunately, the

stratigraphic resolution of this study and the small number of veneroid subgenera that originate during the early stages of the recovery make it difficult to test these hypotheses. To my knowledge, such a study has not been attempted for any macroinvertebrate clade following the K/T.

It is difficult to assess the extent to which the morphological and ecological patterns described above correspond to evolutionary change across the K/T boundary. Thorough investigation of the evolutionary effects of the K/T event requires a well-resolved phylogeny, which for the reasons outlined above was not feasible for this study. A phylogenetic approach to this question would make it possible to (1) track sister clades across the boundary event, (2) quantify extinction selectivity and differential recovery according to synapomorphies, and (3) account for the effects of phylogenetic bias in these data via independent contrasts. Preliminary phylogenetic analysis of fossil taxa within the Pitarinae and Meretricinae has already begun and will presumably help to resolve many of these questions.

Conclusions

Veneroids underwent a substantial extinction at the K/T boundary and did not complete their recovery until approximately 12 Myr later. The K/T extinction was not strongly selective according to morphology or ecology, although there was a very slight tendency for victims to have deeper pallial sinuses (i.e., deeper burrowing habits) than survivors. The recovery, in contrast, was extremely biased toward taxa with deeper pallial sinuses (i.e., deeper burrowing habits). Increased predation pressure or the refilling of vacated ecological niches after the K/T may have forced veneroids into deeper burrowing habits. Patterns of extinction and recovery in morphospace indicate that the recovery proceeded in a step-by-step fashion, starting from the area of morphospace immediately above the area occupied by the survivors and diffusing outward. Invasion of novel morphospace began during the first interval of the recovery (65–61.3 Ma). For veneroids, the morphological and ecological importance of the K/T event is linked to the recovery interval, rather than the

extinction itself. Differential recovery of taxa after mass extinction can affect ecological trends independently of whether the extinction itself is selective. These results emphasize the importance of examining both extinctions and recoveries when attempting to understand the ecological and evolutionary impacts of mass extinctions.

Acknowledgments

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