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

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*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 paleoen-
vironments, makes the veneroids an ideal
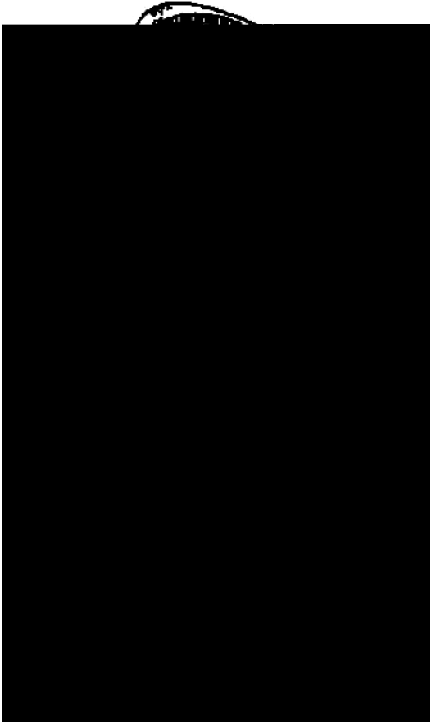clade in which to study the relative influence

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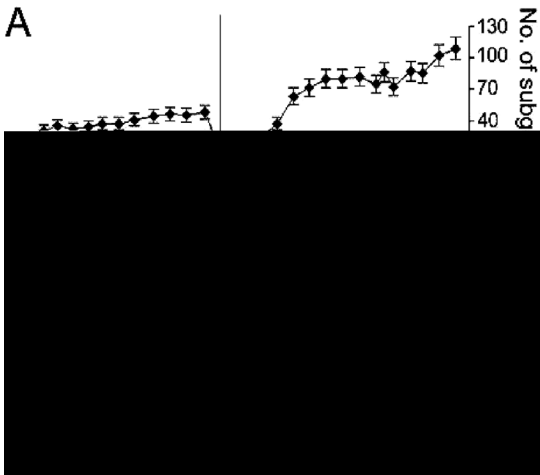
FIGURE 2. Taxonomic diversity patterns in veneroids. A, Global subgeneric diversity measured as the number of taxa crossing boundary intervals. Error bars are approximate and represent the square root of the number of taxa crossing each boundary (Foote 1993). B, Estimated per-taxon extinction rate (q)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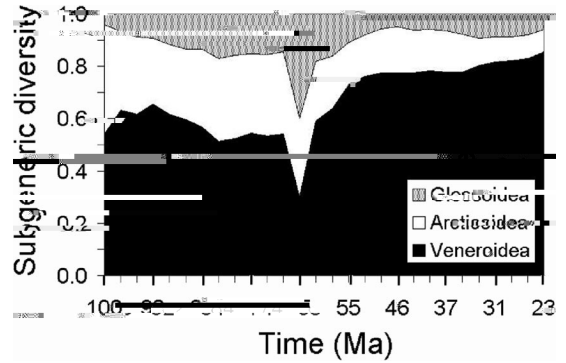


FIGURE 3. Plot of proportional subgeneric diversity for the three superfamilies examined in this study: Glossoidea, Arcticoidea, and Veneroidea.

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
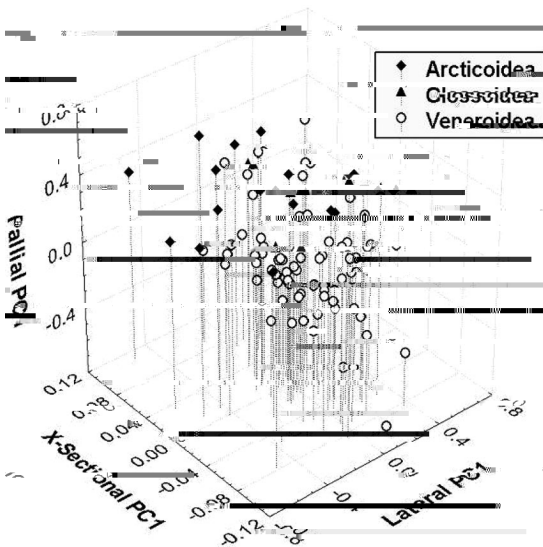
FIGURE 4. Three-dimensional morphospace constructed from the first principal component axes from the lateral shell (Lateral PC1), cross-sectional shell (X-Sectional PC1), and pallial line (Pallial PC1) analyses. Points represent subgenera and are categorized according to superfamily. Subgenera with deeper 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: $r_{559}$ 5 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 midrange 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
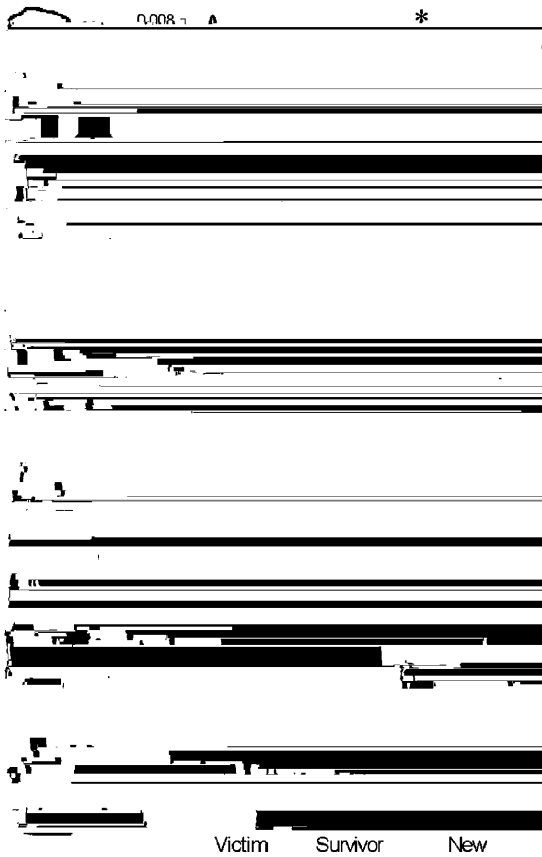
FIGURE 5. Mean (±SE) of three PCA measures of morphology, comparing K/T victims, survivors, and new taxa. A, Lateral PC6. No significant difference was recorded between victims and survivors ($t_{19,9}$ 5 0.93, $p$ . 0.05) after Bonferroni correction. Survivors have significantly lower values of Lateral PC6 than new taxa ($t_{9,29}$ 5 22.83, $p$ 5 0.04) after Bonferroni correction. B, Pallial PC1. No significant difference was recorded between victims and survivors ($t_{15,8}$ 5 22.14, $p$ . 0.05) after adjustment for multiple comparisons. Survivors have significantly higher values of Pallial PC1 than new taxa ($t_{8,28}$ 5 3.31, $p$ 5 0.02) even after adjustment for multiple comparisons. C, X-Sectional PC4. No significant difference was recorded between victims and survivors ($t_{19,9}$ 5 20.23, $p$ . 0.05) after Bonferroni correction. No significant difference was recorded between survivors and new taxa ($t_{9,29}$ 5 22.96, $p$ 5 0.06) after Bonferroni correction.
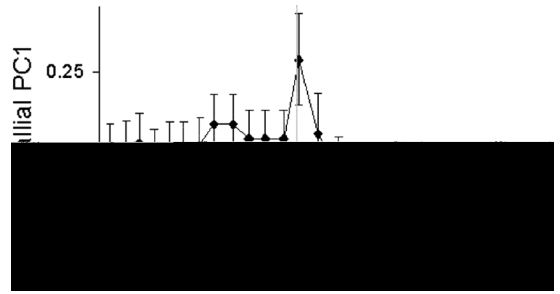


FIGURE 6. Burrowing depth of veneroids through time. Mean (±SE) of Pallial PC1 from the Late Cretaceous to early Cenozoic.

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

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 ($t_{9,29}$ 5 22.83, $p$ 5 0.04) and higher values of Pallial PC1 ($t_{8,28}$ 5 3.31, $p$ 5
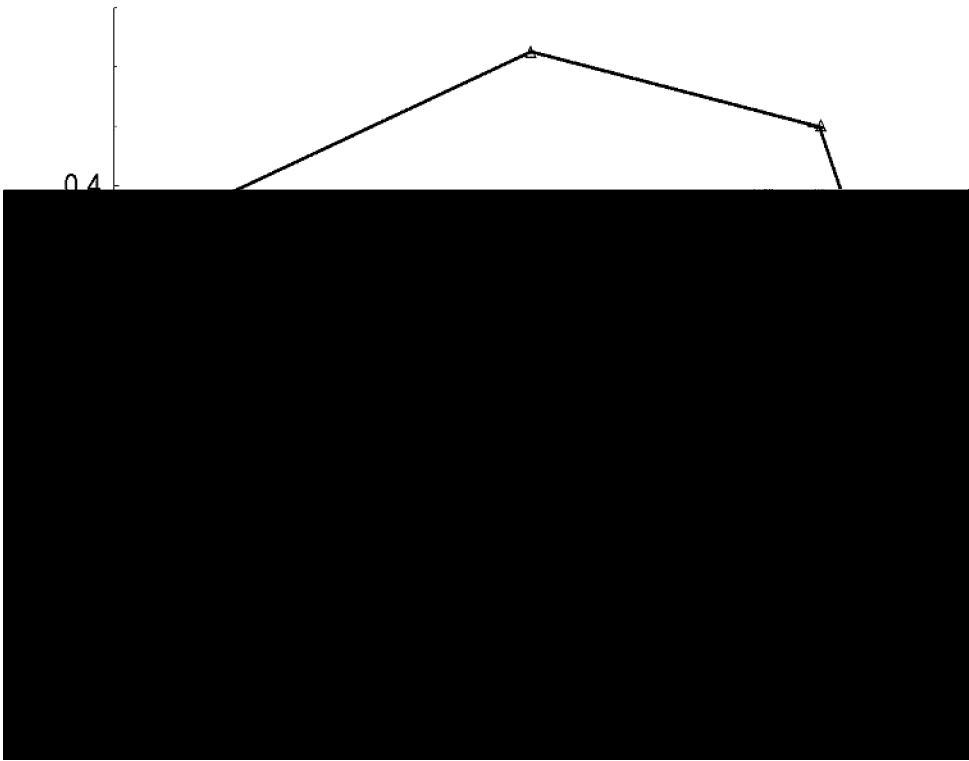
FIGURE 7. Extinction selectivity and differential recovery of subgenera along P
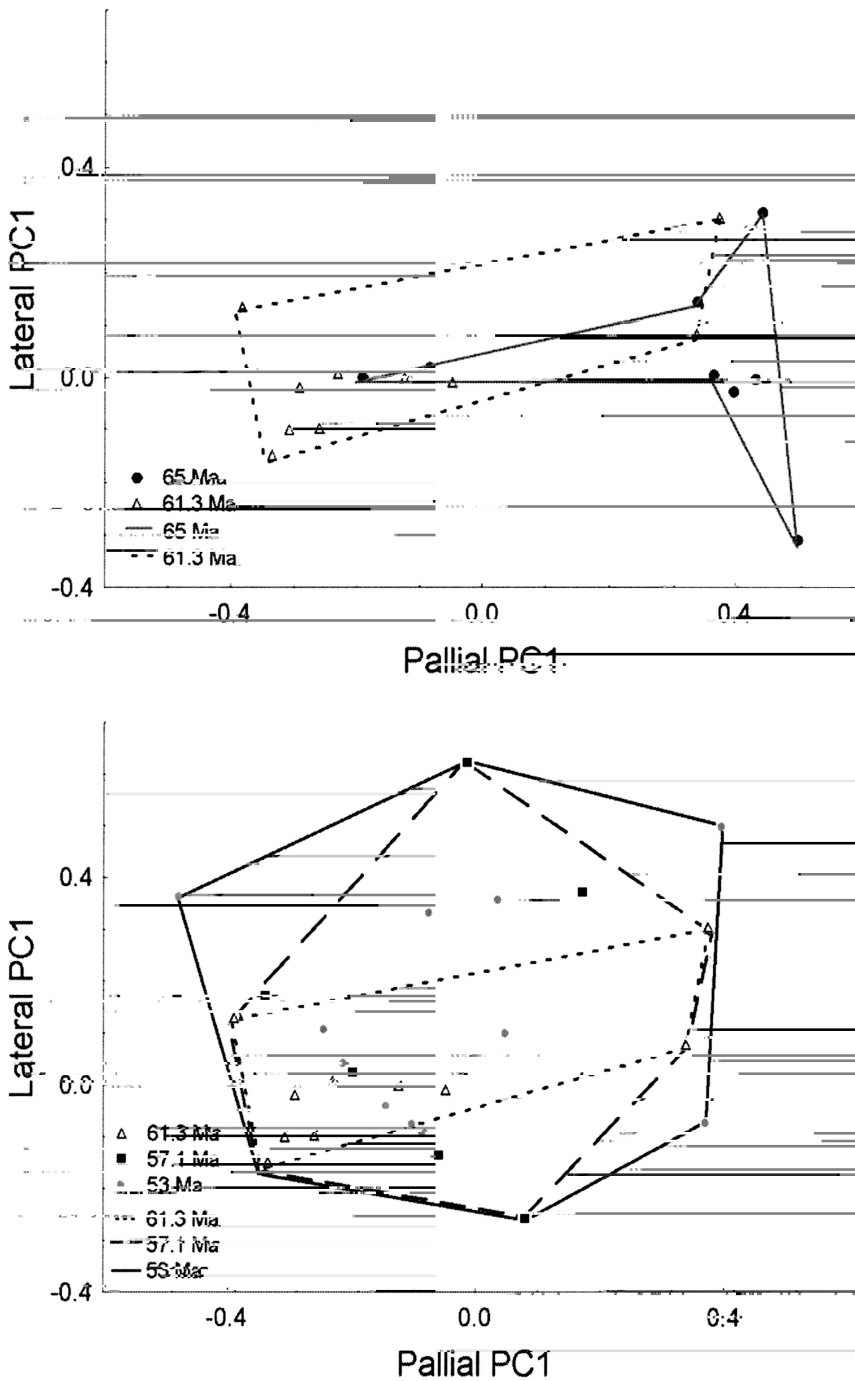
FIGURE 8. Refilling of morphospace during the K/T recovery. Top, Points represent the K/T survivors (65 Ma) and taxa that originated during the first interval of the recovery (61.3 Ma). Outlines represent the entire range of survivors (65 Ma) and taxa that originated during the first interval of the 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) ex

subfamilies Pitarinae and Meretricinae are di-
versifying particularly rapidly throughout
this interval and are contributing dispropor-
tionately to this pattern. It is difficult to pin-

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 re-

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

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