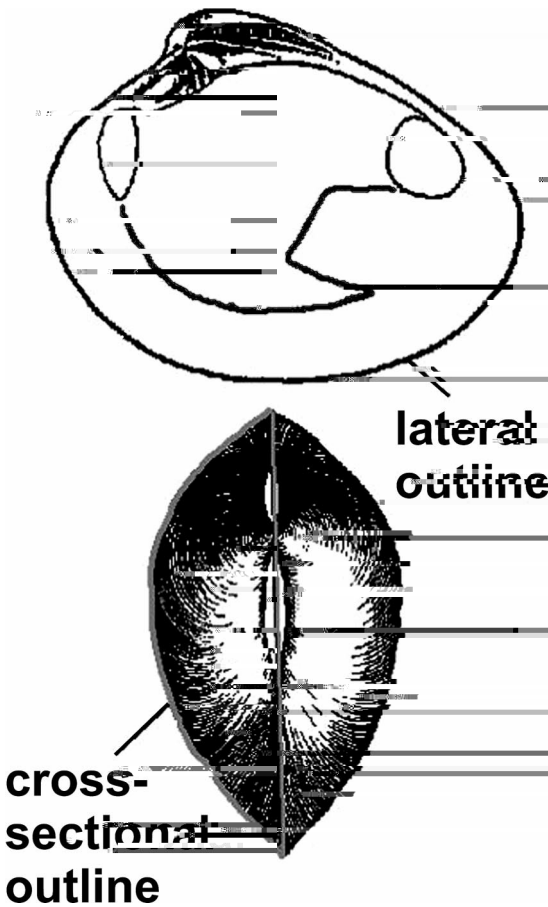valves from California and Japan. The concept

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
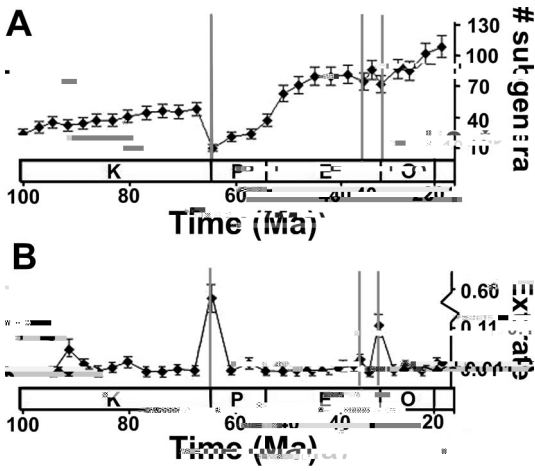
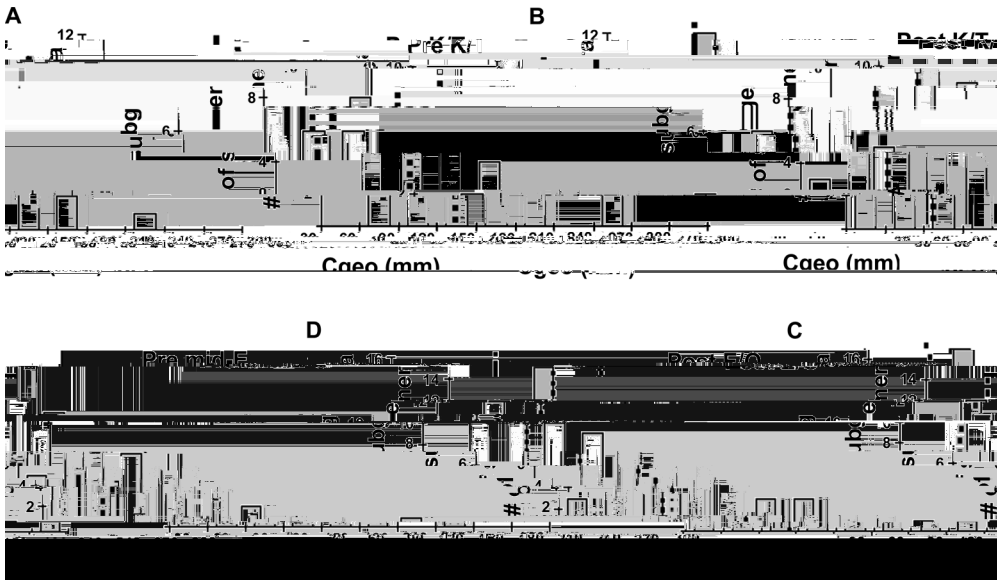FIGURE 2. A, Diversity patterns in veneroids. Global
subg

FIGURE 3. Size frequency distributions for veneroid subgenera that occur before the K/T extinction (A), after the

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 ($t_{46,11} = -2.6$; $p = 0.01$).
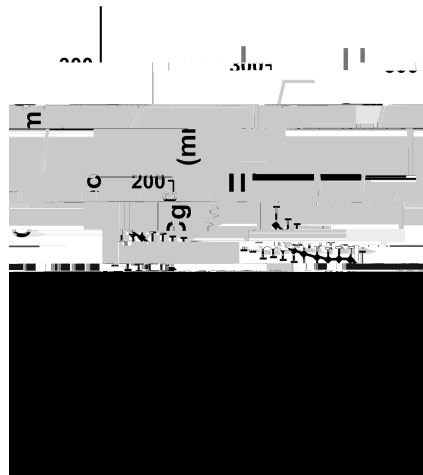

FIGURE 5. Mean (±SE) centroid size (C_{geo}) through time. Gray lines represent the maximum and minimum values for C_{geo} through time. The three dashed lines represent the K/T, mid-E, and E/O extinctions.

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.

pears 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

vated 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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