Paleobiology, 22(3), 1996, pp. 436–452

The roles of mass extinction and biotic interaction in large-scale replacements: a reexamination using the fossil record of stromboidean gastropods

Kaustuv Roy

Abstract.—The macroevolutionary processes underlying large-scale biotic replacements are still poorly understood. Opinion remains divided regarding the roles of mass extinction, biotic interaction, and environmental perturbations in these replacement events. Previous attempts to test replacement hypotheses have largely focused on taxonomic diversity patterns. Taxonomic data alone, however, provide little insight about ecological interactions and hence other approaches are needed to understand mechanics of biotic replacements. Here I propose a conceptual model of replacement based on predation-mediated biotic interactions, and attempt a test using analysis of the Cenozoic replacement of the gastropod family Aporrhaidae by a closely related group, the Strombidae.

Taxonomic, morphologic, and geographic data analyzed in this study all suggest a replacement of aporrhaids by strombids following the end-Cretaceous mass extinction. While most of the taxonomic replacement was associated with a mass extinction, some replacement also occurred during background times and was mediated by higher origination rates in strombids rather than by higher extinction rates in aporrhaids. Morphologically, the replacement was largely confined to the portion of the morphospace unaffected by the end-Cretaceous extinction. At a global scale, the geographic overlap between the two groups declined through the Cenozoic, reflecting increasing restriction of aporrhaids to colder, temperate waters while strombids flourished in the tropics. However, at a finer geographic scale a more mosaic pattern of replacement is evident and coincides with Eocene and Oligocene climatic fluctuations.

The results of this study suggest that mass extinction, long-term biotic interaction, and environmental change can all play significant roles in biotic replacements. Since the relative importance of each factor would vary from one event to another, an understanding of the general nature of large-scale biotic replacements requires a knowledge of the relative intensities of each of these processes.

Kaustuv Roy. Department of Biology, 0116, University of California, San Diego, 9500 Gilman Drive, La Jolla, California 92093-0116

Accepted: February 20, 1996

Introduction

The replacement of one major group of organisms by another has been a recurrent feature in the history of life. While a number of such replacements have been documented, little is known about the underlying evolutionary mechanisms. In particular, the role of biotic interactions in replacements is still debated (see Benton 1987, 1991 for review). While some workers have argued that ecological competition plays a negligible role in large-scale replacements (e.g., Raup et al. 1973; Gould and Calloway 1980; Benton 1987, 1991; Masters and Rayner 1993), others have postulated a more central role for biotic interaction (Stanley and Newman 1980; Krause 1986; Jackson 1988; Maas et al. 1988; Miller and Sepkoski 1988; Rosenzweig and McCord 1991; Lidgard et al. 1993; Van Valen 1994; also see discussion in Allmon 1994). A similar debate also exists regarding the role of mass extinctions in biotic replacements. The common position in this regard has been that mass extinctions are important in mediating replacements as they reduce the dominance of established groups and hence provide other taxa a chance to radiate (e.g., Benton 1987, 1991; Jablonski 1989; Hallam 1990; Rosenzweig and McCord 1991). Some workers, however, remain skeptical, and such a role for extinction has recently been challenged from a conceptual perspective (Masters and Rayner 1993).

A significant obstacle to resolving this debate is methodological. Most of the debate on large-scale replacements is based either on conceptual arguments or on taxonomic diversity patterns (e.g., Gould and Calloway 1980; Benton 1987, 1991; Masters and Rayner 1993).

0094-8373/96/2203-0010/$1.00

However, taxonomic data may be inadequate for addressing these kinds of questions as they reveal little about ecological interactions (Vermeij 1987; Jackson 1988). Important insight into this problem can be gained only by adding other kinds of data dealing with the morphology, biogeography, functional morphology, and relative abundance of the organisms involved in the biotic replacements. The few studies that have investigated replacement events using such data (e.g., Krause 1986; Maas et al. 1988; Rosenzweig and McCord 1991, and Lidgard et al. 1993) have inferred biotic interactions to be important.

This paper has two main objectives: (1) to formulate a conceptual model of long-term replacement that incorporates biotic interactions, mass extinctions, and environmental change, and (2) to test this model through the analysis of one replacement event, the Cenozoic replacement of the marine gastropod family Aporrhaidae by the Strombidae, using a combination of taxonomic, morphologic, functional, and geographic data.

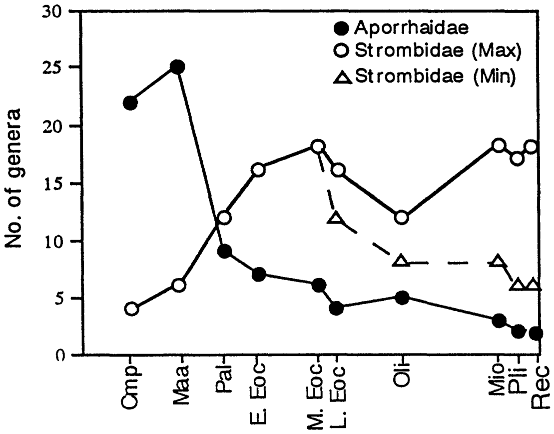

FIGURE 1. Taxonomic diversity of Aporrhaidae and Strombidae from Campanian to Recent. Taxonomic diversity is defined as the total number of genera present during any given time period and has been plotted at the end of each time interval. The timescale is that of Harland et al. (1990), with abbreviations as follows: Campanian (Cmp), Maastrichtian (Maa), Paleocene (Pal), early Eocene (E. Eoc), mid-Eocene (M. Eoc), late Eocene (L. Eoc), Oligocene (Oli), Miocene (Mio), Pliocene (Pli), and Recent (Rec). The diversity of strombids was estimated using two different taxonomic schemes (see text) leading to maximum (open circles) and minimum estimates (open triangles).

The families Aporrhaidae and Strombidae (along with Struthiolariidae and Seraphsidae) belong in the superfamily Stromboidea, a group of marine gastropods characterized by a highly modified apertural margin. The aporrhaids evolved during the latest Triassic and were an important component of the late Mesozoic marine gastropod fauna (Roy 1994). Strombids probably evolved from the aporrhaids during the Cenomanian–Turonian but remained at very low diversity for the rest of the Cretaceous. The end-Cretaceous (K/T) mass extinction removed about 76% of aporrhaid genera while strombid diversity was unaffected. Following the extinction, the early Cenozoic saw a rapid taxonomic radiation of strombids accompanied by a decline in aporrhaid diversity (Fig.1). During the Cenozoic the strombids became the dominant member of the superfamily Stromboidea and appear to have replaced aporrhaids both taxonomically as well as geographically. In modern oceans strombids are an important component of shallow-water molluscan faunas in tropical and subtropical areas while the four extant species of aporrhaids (in two genera) have a restricted distribution, mainly in the temperate Atlantic. The two other members of this superfamily, Seraphsidae and Struthiolariidae, have been excluded from this analysis as there is no indication that they were involved in the replacement event. The struthiolariids are an exclusively Southern Hemisphere group that never geographically overlapped with the strombids. The seraphsids, on the other hand, are a tropical group and did coexist with the strombids. However, the only surviving genus is a burrower in sand and although its ecology is poorly known (see Jung 1974), seems to have a life habit distinct from that of strombids or aporrhaids, especially with respect to the functional and behavioral parameters outlined below.

The data for this study come from two primary sources: (1) collections in the National Museum of Natural History, Washington D.C.; U.S. Geological Survey, Reston, Virginia; Natural History Museum of Los Angeles County; Natural History Museum, London; Museum National d'Histoire Naturelle, Paris; and Museum of the University of West Indies, Kingston, Jamaica; and (2) extensive literature search.

The Monophyly Question

Do the groups involved in biotic replacements need to be monophyletic? A number of well-known examples of biotic replacements involve nonmonophyletic taxa (e.g., gymnosperms vs. angiosperms, Cambrian vs. Paleozoic marine invertebrates, dinosaurs vs. mammals; see Benton 1987, 1991 for other examples). However, Benton (1991) has recently argued that postulated biotic replacements must involve only monophyletic groups. The justification of this position appears to be that only monophyletic clades represent "natural" groupings of taxa and hence are the sole units that can be used to study "real" macroevolutionary dynamics. However, I do not consider it necessary to invoke the strict monophyly criterion in studies of biotic replacement; replacements involving paraphyletic groups are just as valid and interesting as those involving monophyletic groups. First, recent simulation studies have suggested that, given the nature of the fossil record, paraphyletic groups may, in fact, be better at capturing large-scale macroevolutionary patterns than monophyletic groups (Sepkoski and Kendrick 1993). Second, paraphyletic groups often have characteristic functional and behavioral traits that make them valid ecological units (Sepkoski 1984, 1987; Van Valen 1985; Valentine 1990; Vermeij 1994). Of course, several workers have criticized this position by arguing that the boundaries of paraphyletic groups depend on the subjective judgments of systematists and hence such groups have questionable validity (see Smith and Patterson 1988; Benton 1991; Smith 1994). In the present context this criticism appears unjustified as ecological and phylogenetic groupings represent different entities and should never be equated (see Eldredge 1985, 1986, 1989, 1992). For example, aporrhaid gastropods (a paraphyletic group) are characterized by a leaping mode of locomotion and a set of behavioral traits that are absent from all other gastropods (see discussion below). Strombid gastropods, the monophyletic clade that descended from the aporrhaids, on the other hand, are also characterized by a leaping mode of locomotion, but with fundamentally different mechanics, and a different set of behavioral attributes that are unique to them (see below). If we were interested in studying the evolution of leaping vs. crawling locomotion in gastropods then of course the monophyletic group Stromboidea would be the unit of choice. However, the paleoecological and evolutionary consequences of the origin of a fundamentally different style of leaping locomotion in one subset of the clade in question cannot be studied without the use of a paraphyletic group. Note that while there is phylogenetic continuity between the two groups in question, they can be easily separated into two ecological units based on a set of explicit and objective functional and behavioral traits (see Jablonski and Bottjer 1990 for a similar argument regarding the crinoid order Isocrinida; Hay 1994 and references therein for a discussion of the ecological importance of polyphyletic functional groups; also Vermeij 1994). Rosenzweig and McCord (1991) have argued that even the somewhat old-fashioned concept of grades often reveals broad sets of constraints operating in a group at any given time in its evolutionary history and hence the replacement of one grade of organisms by another can provide insights into mechanisms of faunal replacements.

Thus, as long as the groups involved are defined on the basis of an explicit and objective set of ecological, functional, and/or morphological parameters, quantification of empirical patterns of biotic replacement is not contingent on the presence of a phylogenetic framework. Phylogenetic hypotheses, however, serve an important role once such patterns of biotic replacement have been quantified as they can then be used as tests of potential macroevolutionary processes driving the patterns. For example, the role of species/clade selection in biotic replacements (see Stanley 1979; Williams 1992) is still unresolved and obviously can be addressed only within a phylogenetic framework.

A Conceptual Model of Biotic Replacements

The models of competition traditionally used in paleontological studies (either implicitly or explicitly) have been derivations of the Lotka-Volterra model (i.e., direct competition) in which the success of one group drives the gradual demise of the other. As has been correctly pointed out, not only are there serious theoretical problems in scaling up this type of competition into macroevolutionary time (although see Sepkoski 1994) but there is also little evidence for competitive extinction in the fossil record (see Benton 1987, 1991; Wiens 1989; Rosenzweig and McCord 1991). While the role of direct competition remains questionable, effects of alternative modes of biotic interactions on evolutionary replacements remain underexplored. One example of such interactions that has been explored in this context is ecological advantages due to incumbency (e.g., Valentine 1990; Hallam 1990, Rosenzweig and McCord 1991). However, a second type of interaction that has received little attention from the evolutionary perspective is indirect interaction due to shared predators, also called "apparent competition" (see Holt 1977; Jeffries and Lawton 1984; Holt and Lawton 1994). Theoretical as well as experimental investigations of this type of interaction have revealed that, on ecological timescales, the effects of two species sharing a common enemy can often be identical to conventional forms of interspecific competition (see Holt and Lawton 1994, and references therein). The conceptual model outlined below attempts to integrate this notion of interactions into long-term biotic replacements.

Consider a group of species vulnerable to certain predators but possessing an exaptation that provides some defense against these enemies. Everything else being equal, on evolutionary timescales this predator-prey system would be at dynamic equilibrium so that both predators and prey should have characteristic origination and extinction rates. Let us assume that in some portion of the geographic range of the first set of species a second group evolves from it. Let us further assume that the new group of species is characterized by a derived set of attributes (morphological and/or behavioral) that is better at resisting predation compared to the first group. In areas where the two groups overlap they will experience shared predation, which can lead to either a reduction in abundance of one species or its elimination from that community (Jeffries and Lawton 1984 and references therein). A point worth noting here is that the evolution of a particular anti-predatory trait in a group of species can often impose constraints on various aspects of their ecology (see Jeffries and Lawton 1984), and hence groups of species sharing similar ways of avoiding predators can often converge on similar ecological requirements. In the present scenario, as far as the first group is concerned, the effects of this "apparent competition" (sensu Holt 1977) may be partially offset by the advantages of ecological incumbency especially if the ancestral group is significantly more diverse taxonomically and widespread geographically. However, if the system is sufficiently perturbed (e.g., through a mass extinction), and the incumbent group loses its "home-field advantage" (sensu Pimm 1991), the effects of indirect competition through the sharing of enemies would intensify, with the second group being less vulnerable to predation. This, over evolutionary time, could lead to the replacement (partial or total) of the first group.

The above model is consistent with the dynamics of "apparent competition" (see Holt and Lawton 1994) and with advantages of incumbency in ecological systems and on geological timescales (e.g., Pimm 1991; Rosenzweig and McCord 1991; Massot et al. 1994). Finally, it makes evolutionary sense given the observation that predation has been an important driving force in the history of marine life (see Vermeij 1987, 1994). Also, since it makes certain predictions about the replacement patterns, it is testable using paleobiological data. The main predictions of the model include the following: (1) the groups involved in the replacement must have traits (functional, behavioral, or both) that demonstrably resist certain types of predation, and they must have similar ecological requirements; (2) the major phase of replacement must follow a mass extinction; and (3) the groups involved should overlap geographically. Before these predictions can be tested, two final points need to be addressed. The first involves the question of how the biotic interactions of the type described above would translate into macroevolutionary patterns. This remains a problem given our limited insight regarding speciation mechanisms (see Jackson 1988). However, it has been argued that the kinds of interactions discussed here are more likely to translate into macroevolutionary trends through speciation rate advantages rather than through extinctions (see Vermeij 1987, 1994; Rosenzweig and McCord 1991; Allmon 1994). Thus, replacements of this type should be driven by increased speciation in the replacing group. Finally, given the timescales involved, replacement models of the nature discussed here must consider the effects of long-term fluctuations in environmental parameters. These effects would vary from event to event but, in general, should be manifested as changes in the geographic distribution of the species involved, which in turn should affect the intensity of biotic interactions.

Aporrhaidae and Strombidae

Ancestry and Ecology.—The family Aporrhaidae first appeared in the latest Triassic, and the group reached maximum taxonomic diversity and a global distribution during the Cretaceous (Roy 1994). The ancestry of aporrhaid gastropods is not clear and affinities with Cerithiidae and Loxonematoidea have been proposed (see Roy 1994). The aporrhaids are generally considered to be ancestral to the family Strombidae, which originated during Cenomanian–Turonian times. As discussed later, strombids were restricted both taxonomically and geographically during the rest of the Cretaceous and did not become important until after the end-Cretaceous extinction.

Aporrhaid and strombid gastropods are both characterized by highly modified and expanded apertural margins. Both groups exhibit determinate growth, so that fully developed apertural margins indicate a cessation of growth and attainment of sexual maturity. The exact functional significance of the apertural modifications is not fully understood although they clearly play important roles in avoiding both durophagous and drilling predators and in locomotion (Perron 1978a,b; Merz 1979; Savazzi 1991). Strombids and aporrhaids differ from other gastropods in that they both exhibit a "leaping" style of locomotion, albeit with different mechanics (see below). Both groups are exclusively herbivorous or detritivorous, feeding mainly on macroalgae, epiphytes, and bacterial mats (Perron 1978a for aporrhaids; Geary and Allmon 1990; Savazzi 1991 and references therein for strombids). The living members of Aporrhaidae show a characteristic seasonal burrowing behavior in which they are epifaunal grazers for part of the year while the rest of the year is spent infaunally without feeding (Perron 1978a). Similar seasonal burrowing cycles, which are otherwise rare in marine gastropods, may also be present in certain strombid species (Percharde 1968, 1970; Perron 1978a; Geary and Allmon 1990 and references therein) although detailed ecological observations are lacking. The two families, however, differ substantially in their environmental distributions. Recent strombid species occur exclusively in shallow waters of tropical and subtropical areas (Clench and Abbott 1941; Abbott 1960; Geary and Allmon 1990), and fossil species appear to show similar preferences (Savazzi 1991; this study). Recent aporrhaids, on the other hand, are mainly confined to temperate waters and have extensive depth ranges (Perron 1978a; Kronenberg 1991), whereas fossil species were globally distributed during the Mesozoic (Roy 1994). At present the only geographic overlap between the two groups is off West Africa but even here their bathymetric distributions seem to be disjunct as the aporrhaids are apparently restricted to deeper waters (55 meters and deeper, see Kronenberg 1991).

Feasibility of Interaction.—The discussion so far has highlighted the fact that the close phylogenetic relationship of the two families, Aporrhaidae and Strombidae, has resulted in the sharing of a number of unique ecological and functional traits. There are, however, important differences between the two groups, and it is these differences that provide the context for biotic interaction between them. While aporrhaids and strombids both share a "leaping" style of locomotion, the mechanics of the process differ significantly for the two groups. Locomotion in stromboidean gastropods can be divided into three types, each associated with a characteristic style and rate: (1) normal locomotion, i.e., movements during feeding and related activities in the absence of pred-

TABLE 1. Comparison of locomotion rates (cm/min) in strombid and aporrhaid gastropods.

	Range	Mean	SD
Normal locomotion			
Strombid	1.1–7.8	2.8	2.8
Aporrhaid	0.5–2.3	1.19	0.62
Escape locomotion			
Strombid	33.2–94.1	67.4	22.7
Aporrhaid	7–24	14.1	5.04

Data for strombids from Berg (1974), for aporrhaids from Perron (1978b). Strombid values based on mean rates for *S. mutabilis, S. maculatus, S. gibberulus, S. luhuanus,* and *S. lentiginosus,* which are comparable in size to *A. occidentalis,* the basis for aporrhaid data. Values for four species of *Lambis* listed in Berg (1974) are excluded because they are much larger in size. Their inclusion would make the difference in escape rates even more pronounced.

ators; (2) escape locomotion, i.e., rapid movement away from predators (mainly molluscan); and (3) shell righting, a response elicited when shells are overturned and vulnerable to predation. Mechanics and rates of each of these styles of locomotion have been discussed and quantified experimentally by a number of workers (see Haefelfinger 1968; Perron 1978b for aporrhaids; and Berg 1974, 1975 for strombids). These studies suggest that the primary difference between aporrhaid and strombid locomotion centers on the use of the operculum. The operculum is not well developed in aporrhaids and plays no role in locomotion; normal and escape locomotion and shell righting are all achieved through various movements of the foot. The strombids, on the other hand, have a very well-developed operculum that plays a significant role in locomotion. Normal locomotion in some strombids is achieved through extensions of the footstalk and resembles that of aporrhaids (e.g., *Strombus maculatus, S. mutabilis*) whereas in others the operculum is used in conjunction with movements of the footstalk (e.g., *S. gibberulus* [see Berg 1974]). For species of comparable size, average rates of normal locomotion are somewhat higher for strombids compared to aporrhaids (Table 1).

The difference between the two families becomes most obvious in the rates of escape locomotion. Data from Perron (1978b) and Berg (1974) clearly demonstrate that the rate of escape locomotion for *Arrhoges occidentalis* is strikingly slower than that of various strombid species (Table 1). This significant difference in rates of escape appears to be due largely to the fact that strombids use their large operculum as a lever to generate a series of very rapid leaps away from the predator while aporrhaids, lacking a well-developed operculum, are not capable of moving in such a manner or so rapidly. It should be pointed out that while the strombids show some of the most specialized and effective escape responses known among gastropods, the escape rates for aporrhaids are fast compared to most gastropods.

Predatory mollusks have played an important role in the Mesozoic–Cenozoic evolution of gastropods (Vermeij 1987). The evolution of the strombid style of escape locomotion is undoubtedly one way to reduce the cost of defense against slow-moving molluscan predators and hence should provide significant ecological benefits, which, given the replacement model discussed above, should lead to the replacement of ecologically similar groups lacking the exaptation.

Taxonomic Diversity Patterns

A Note on Taxonomy.—For the purpose of this study, taxonomic diversity is defined as the total number of genera present during any given time interval. The taxonomy of fossil strombids needs serious revision and some of the problems are similar to those discussed elsewhere for aporrhaids (see Roy 1994). An additional problem involves the "pull of the Recent" (sensu Raup 1979) and primarily concerns the genus *Strombus.* This extant genus has been divided into a number of subgenera (e.g., 12 subgenera in the Indo-Pacific [see Abbott 1960]) largely on the basis of a set of characters not easily recognizable in the fossil record (e.g., shell color, subtle differences in ornamentation, and verge, operculum, and radular characters). Thus, it is not clear how these subgeneric groupings compare to the extinct strombid species-groups (i.e., genera) defined mainly on shell shape. In order to assess the potential bias introduced by such taxonomic problems, I computed the diversity of the group using minimum and maximum estimates (Fig. 1). The minimum estimate treats *Strombus* as one genus and omits two other very poorly known late Eocene genera (*Cowlitzia* and *Laevella*) as well as two extant subgenera of *Lambis*; the maximum estimate not only includes the Eocene taxa but treats all Recent subgenera of *Strombus* and *Lambis* as genera. For the latest Cretaceous and Tertiary, the minimum estimate is 26 genera while maximum estimate is 41 genera. These two values bracket the potential error associated with estimating strombid diversity due to taxonomic problems. The minimum value is, in fact, closer to that of Savazzi (1991) who estimated 25–30 genera of Tertiary strombids. For the aporrhaids, I divided Campanian–Recent aporrhaids into 25 genera using an internally consistent taxonomic framework (see Roy 1994).

Results.—The strombids and aporrhaids show reciprocal temporal trends in taxonomic diversity (Fig.1). The aporrhaids achieved highest taxonomic diversity during the Maastrichtian (see Roy 1994 for the Mesozoic history of the group), suffered heavily during the K/T extinction (76% extinction at the generic level), and continued to decline throughout most of the Cenozoic. The strombids, on the other hand, exhibited low diversity during the Cretaceous and were unaffected by the K/T extinction. They radiated rapidly following the extinction event, achieved maximum diversity during middle Eocene, and either declined in diversity thereafter (using the minimum estimate of diversity) or declined during the late Eocene and Oligocene and then rebounded to mid-Eocene levels (using the maximum estimate).

The major phase of replacement (at least from the global taxonomic perspective) occurred immediately after the K/T extinction, followed by a steady rise in strombid diversity and an associated decline in aporrhaid diversity. It appears that the taxonomic replacement of aporrhaids by strombids was essentially complete by the end of the Eocene, and for the rest of the Cenozoic relatively stable proportions were maintained (Fig. 1). While the two different diversity estimates provide somewhat different pictures of strombid history during the late Paleogene and the Neogene, the differences between the estimates clearly postdate the replacement event. Thus, the patterns of replacement (taxonomic, morphologic, and geographic) discussed in this paper should be robust to these kinds of taxonomic problems.

The reciprocal taxonomic diversity trends show that the major phase of replacement was associated with the K/T extinction but do not provide much insight into the dynamics of replacement during Paleocene and Eocene. Such insight can, however, be obtained from a comparison of the origination and extinction rates of the two groups (Fig. 2), which shows that: (1) although the diversity of aporrhaids was drastically reduced by the K/T extinction the group showed a substantial taxonomic rebound during the Paleocene, and (2) the post-Maastrichtian taxonomic replacement was driven primarily by the higher origination rates of strombids as the extinction rates for both groups remained comparable.

Morphological Diversity Patterns

Methods.—At present there is no single, standard metric that can be used to measure morphologic diversity (Foote 1991a), and hence a number of different approaches have been proposed (see, for example, Runnegar 1987; Gould 1989, 1991; Erwin 1990; Foote 1990, 1991a,b, 1992, 1993; Roy 1994). In this study, I have used 26 shell morphologic characters to define a morphospace for 25 genera of aporrhaids and 37 genera of strombids and to examine changes in patterns of morphospace occupation across the replacement event. Note that I have used the maximum estimate of diversity in this analysis but had to exclude four genera (*Pereiraea, Cowlitzia, Laevella,* and *Sulcogladius*) because of insufficient information. Morphologic analyses based on the minimum diversity estimate (not plotted here) yield essentially the same broad replacement pattern.

The 26 characters used here represent those commonly used to define strombid and aporrhaid genera and include both apertural and non-apertural components. Of the 26 characters, 24 are binary and the remaining two have multiple states that were scaled to unity (Table 2). Q-mode nonmetric multidimensional scaling (MDS) based on a euclidean distance matrix was used to quantify the strombid-aporrhaid morphospace (see Roy 1994 for a description of this method). The scores of the four-dimension-

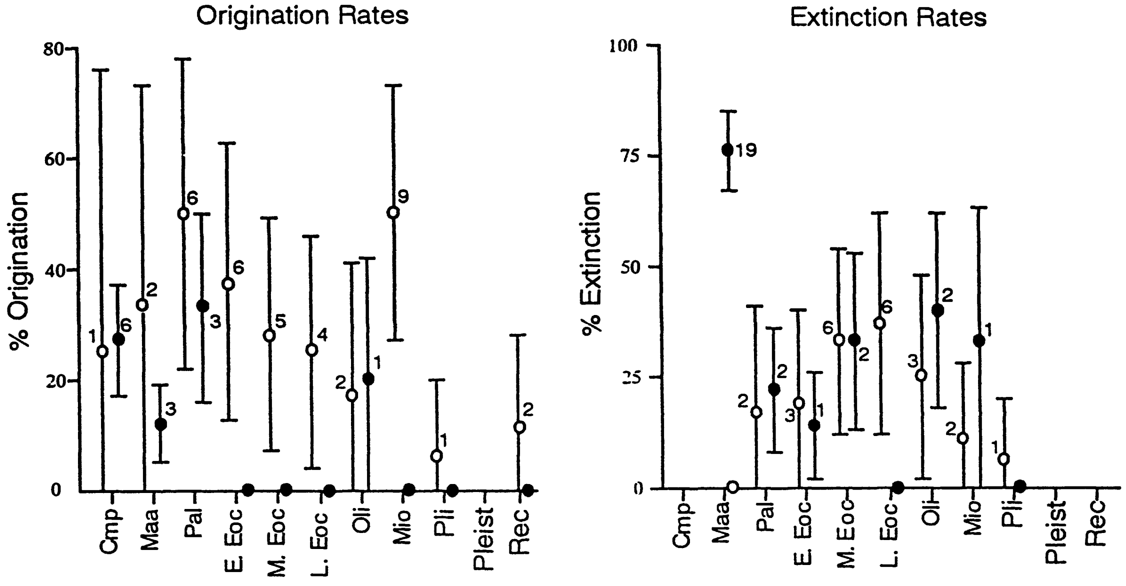

FIGURE 2. Origination and extinction rates of Strombids (open circles) and aporrhaids (solid circles) from the Campanian to the Recent. Rates expressed as a percent of standing diversity. The actual numbers of originations and extinctions are shown in each case. The error bars represent 95% confidence intervals, calculated following Raup (1991).

al MDS were sorted stratigraphically and used to visualize the temporal pattern of morphologic change. The scores were then used to quantify the changes in morphologic diversity of the two groups through time. Morphologic diversity is defined here as the geometric mean of the ranges of ordination scores (Foote 1991a; Roy 1994).

Results.—The first two dimensions of the four-dimensional MDS are plotted in Figure 3. These two dimensions separate the taxa main-

TABLE 2. List of morphologic characters used to define the aporrhaid-strombid morphospace.

1. Spire height: high, low (<half length of body whorl)
2. Sides of whorls: angular, rounded
3. Aperture shape: elongate, semicircular
4. Anterior process: long, short
5. Anterior process: straight, curved
6. Posterior canal: long, short or absent
7. Spiral body chords extending to apertural process: present, absent
8. Callus on spire: present, absent
9. Posterior process extending beyond spire: present, absent
10. Apertural callus: present, absent
11. Anterior process width: narrow, broad
12. Lip expansion: digitate unexpanded, digitate expanded, nondigitate unexpanded, nondigitate expanded
13. Thin web between digits: present, absent
14. Posterior margin of aperture extended: present, absent
15. Digit extending around body whorl: present, absent
16. Curvature of process perpendicular to apertural plane: strong, weak
17. Apertural margin: single, multidigitate
18. Number of apertural digits: 0 or 1, 2, >2
19. Row of shoulder spines/nodes: present, absent
20. Strombid notch: well-developed, poor or absent
21. Shell shape: elongate, short and stout
22. Axial nodes: strong, weak or absent
23. Inside of outer lip: smooth, with spiral lirae
24. Sculpture: well-developed, poor or absent
25. Sculpture: single type, ornate
26. Apertural extension adnate to spire: present, absent

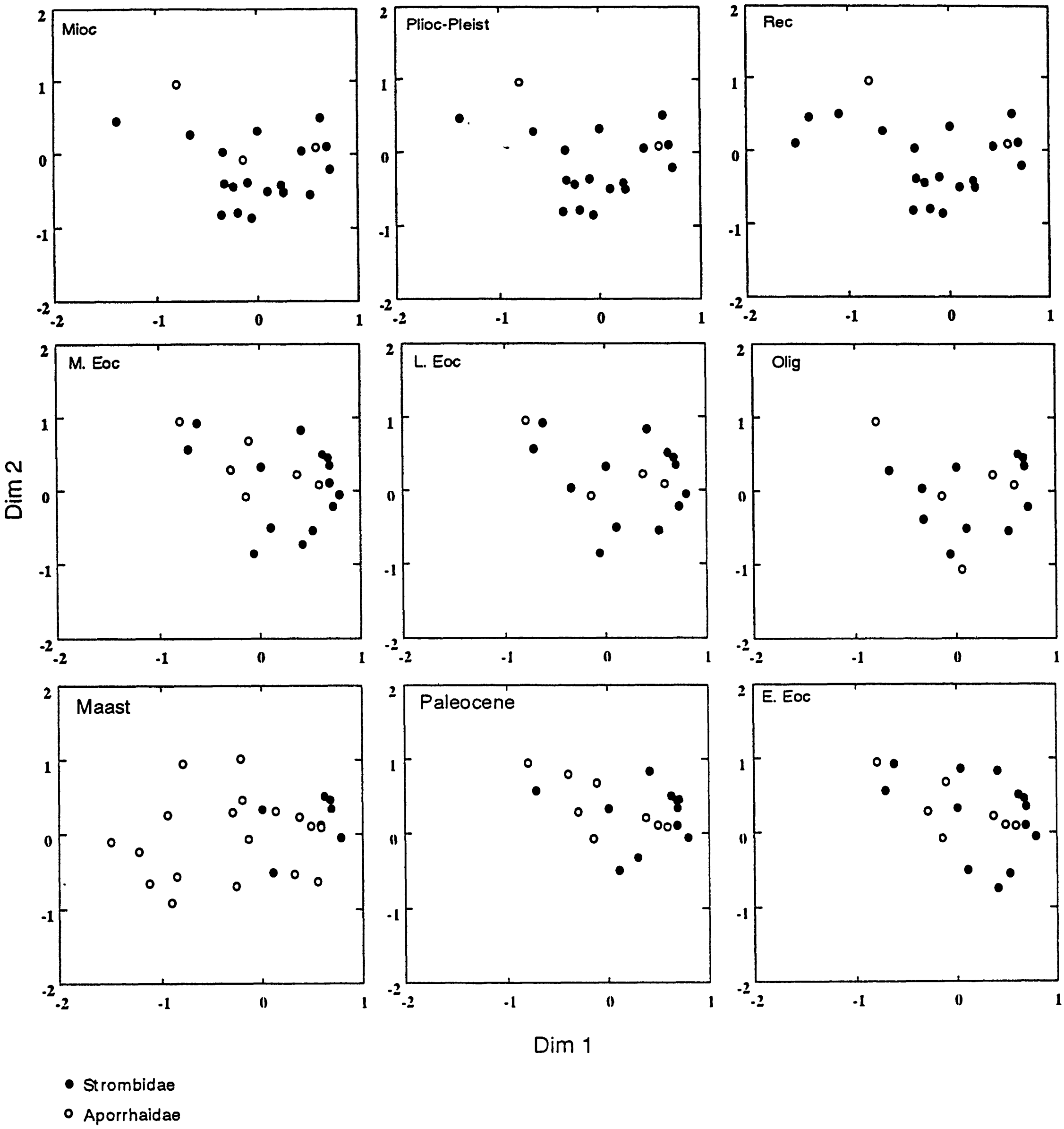

FIGURE 3. Temporal pattern of morphospace occupation exhibited by aporrhaid and strombid genera from Maastrichtian to Recent. The plots show the first two dimensions of a four-dimensional MDS ordination (see text). The ordination was done using the MDS routine in Systat 5.1 (Systat Inc., Evanston, Ill.). These two axes separate the taxa mainly on the basis of the shape of their apertural processes. Note that a substantial part of the aporrhaid morphospace was vacated following the end-Maastrichtian extinction and this part was never recolonized except by the strombid genera *Lambis* (Mioc–Rec), *Millepes* (Rec), and *Harpago* (Rec). The Cenozoic history of the two groups was mainly confined to that part of the morphospace that was relatively unaffected by the Maastrichtian extinction.

ly on the basis of the shape of their apertural processes. The Shepard plot for the ordination was linear and the stress of the final configuration was 0.08, indicating low levels of distortion (see Kruskal 1964). The temporal sequence of morphospace occupation reveals some interesting patterns. During the Maastrichtian, the aporrhaids had high taxonomic diversity and occupied a large segment of the morphospace, while the strombids had low taxonomic diversity and were restricted to a very small segment of the morphospace. The end-Maastrichtian extinction changed the picture drastically by severely reducing the taxonomic and morphologic diversity of the aporrhaids but not affecting the strombids. A large part of the aporrhaid morphospace was cleared by this extinction and this segment was never reoccupied by either group except very late in the history of strombids. In fact, the entire post-Maastrichtian morphologic history of the two groups was played out in the segment of the morphospace that was relatively unaffected by the Maastrichtian extinction. The only exception is a group of three very closely related strombid genera, of which *Lambis* evolved during the late Miocene, while the other two, *Millepes* and *Harpago,* are both extant and appear to lack a fossil record. These three genera are all characterized by a large multidigitate aperture and are convergent on some of the Mesozoic aporrhaid morphologies (e.g., *Harpagodes,* see Roy 1994). Thus the post-Maastrichtian radiation of the strombids, although dramatic from a taxonomic perspective, was restricted to only a small segment of the total morphospace, largely within limits set during the Paleocene.

A similar picture emerges when temporal patterns of morphologic diversity are quantified. In this case the geometric mean of the ranges of scores on the first three axes are plotted in Figure 4. While strombids and aporrhaids do show reciprocal trends in morphologic diversity, the differences are not nearly as striking as in the taxonomic patterns. Aporrhaid diversity decreased following the end-Maastrichtian extinction but then remained virtually stable through the Paleogene and dropped significantly only when diversity dropped to two surviving genera during the Neogene. For the strombids, morphologic diversity increased following the Maastrichtian extinction but then remained remarkably stable through the most of the Paleogene, again indicating that the taxonomic radiation was constrained within a restricted part of the morphospace.

Geographic Patterns

Methods.—The importance of geographic patterns in analyses of biotic replacements has been pointed out in a number of studies (Krause 1986; Maas et al. 1988; Rosenzweig and McCord 1991). However, as discussed by Koch (1987) and Koch and Sohl (1983), quantitative analyses of geographic distributions of fossil taxa are particularly susceptible to sampling problems. As far as this study is concerned, the geographic record is particularly biased during the period immediately following the end-Maastrichtian mass extinction, be-

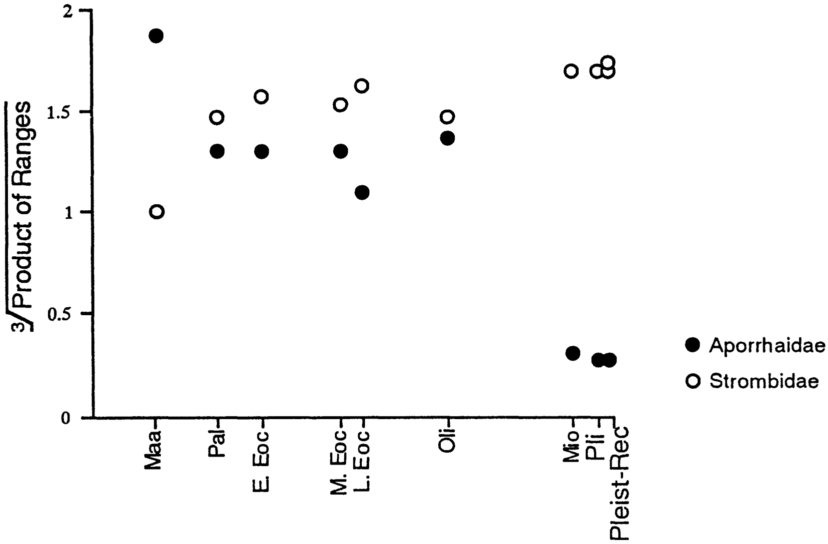

FIGURE 4. Temporal trends in morphologic diversity shown by aporrhaid and strombid genera. Morphologic diversity is defined as the geometric mean of the ranges of scores on the first three MDS dimensions.

TABLE 3. List of geographic divisions used in this study.

1. Gulf and Atlantic Coastal Plain
2. California, Washington, Oregon
3. Mexico and Central America
4. Western Interior Basin
5. Indian subcontinent
6. N. Africa and Arabia
7. W. Africa
8. E. Africa
9. S. Africa
10. N. Europe (north of 45°N)
11. S. Europe
12. Western S. America
13. Caribbean
14. Crimea and adjoining areas
15. China and Tibet
16. Madagascar
17. Brazil, Venezuela
18. Antarctica
19. Australia and New Zealand
20. Japan and adjoining areas
21. Indo-Pacific

cause of the patchy global distribution of Paleocene marine sediments. In order to minimize these problems, I have examined the aporrhaid-strombid replacement pattern using a rather coarse geographic framework that divides the world into 21 geopolitical divisions (Table 3). This approach is very similar to the one used to study the Mesozoic history of aporrhaids (see Roy 1994) and attempts to reduce sampling problems by grouping data over large areas and multiple facies. Since strombid and aporrhaid gastropods are characterized by similar shell mineralogy, microstructure, and overall morphologies, I have assumed that they have similar preservation potentials.

Results.—Figure 5 shows the total number of geographic divisions occupied by each group from Campanian to Recent. The overall pattern parallels that of taxonomic diversity: the number of geographic divisions occupied by the aporrhaids decreased rapidly following the end-Maastrichtian extinction and with minor fluctuations remained low for the rest of the Cenozoic. The strombids, on the other hand, suffered a slight reduction in their total geographic extent following the end-Maastrichtian extinction but quickly rebounded to their pre-extinction level of geographic occupancy and maintained comparable levels for

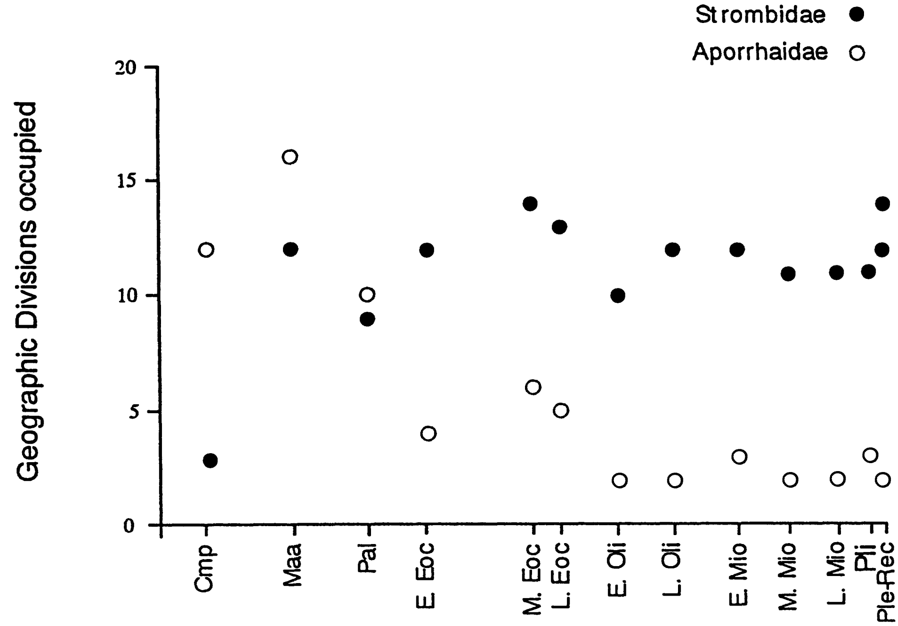

FIGURE 5. Temporal trends in the number of geographic divisions occupied by aporrhaid and strombid gastropods from the Campanian to the Recent. The number of divisions occupied by the aporrhaids fell sharply following the end-Maastrichtian extinction and overall the group was characterized by fairly low values for the rest of the Cenozoic. The geographic occupancy of the strombids was also negatively affected by the Maastrichtian extinction but this group not only quickly rebounded back to pre-extinction levels but maintained comparable levels for the rest of the Cenozoic.

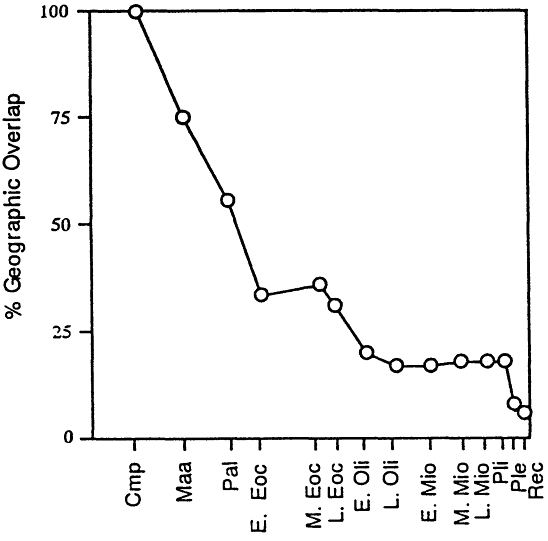

FIGURE 6. Percent geographic overlap between strombid and aporrhaid gastropods from Campanian to Recent. Geographic overlap is defined here as $(D_{sa} / D_s) * 100$, where D_{sa} is the number of geographic divisions containing both strombids and aporrhaids, and D_s is the total number of divisions containing strombids. Thus 100% overlap means that all divisions containing strombids also had aporrhaids (e.g., Campanian) while 0% overlap indicates a total geographic separation.

the rest of the Cenozoic. An examination of the percent geographic overlap between the two groups suggests that they exhibit reciprocal patterns not just taxonomically but also biogeographically (Fig. 6). The geographic overlap between the two groups was severely reduced during a 15-m.y. period immediately following the end-Maastrichtian extinction. For the rest of the Cenozoic the overlap decreased steadily but at much reduced rates and was finally completed during the Pleistocene when strombids disappeared from the northern Mediterranean. As mentioned earlier, the West African coast is now the only place where strombids and aporrhaids coexist but even here they appear to be bathymetrically disjunct.

Although the global pattern shows an increase in strombid geographic distribution during the Cenozoic, and concomitant decrease in aporrhaid distribution, the local patterns can be significantly different. This is illustrated by the local histories of three geographic areas, namely, the Gulf and Atlantic Coastal Plain of North America, northern Europe, and the Indian subcontinent and adjacent Southeast Asia (Fig. 7). All of these areas preserve a relatively continuous (albeit sometimes sparse) temporal record of stromboidean gastropods. In the Coastal Plain, although the taxonomic diversity of the aporrhaids was reduced drastically by the end-Maastrichtian extinction, the strombid radiation was not detectable until the Eocene and the replacement appears to have been completed by the end of Eocene. In contrast, in northern Europe the end-Maastrictian extinction also reduced aporrhaid diversity, but the group rebounded and the major decrease was during the Paleocene, resulting in one surviving aporrhaid genus by the early Eocene. This drop in diversity was accompanied by a rapid taxonomic radiation of the strombids. Strombid diversity, however, declined rapidly during the early Neogene and strombids became extinct in northern Europe by the end of the Miocene. Thus in this area the replacement was never completed and one aporrhaid genus (*Aporrhais*) has survived. A similar situation also holds for southern Europe (not shown), where the aporrhaids have managed to survive despite a Paleogene radiation of strombids. In the Indian subcontinent, however, the replacement of aporrhaids by strombids was rapid and took place immediately after the end-Maastrichtian extinction. Since the Indian subcontinent is one of the few areas with a good Paleocene record, this rapid replacement is probably real and not simply a taphonomic artifact. In the tropical Indo-Pacific area (not shown), only one aporrhaid genus is known from the Maastrichtian, and this became extinct at the end of Cretaceous. Given the poor Cretaceous and Paleogene records present in this area, the low diversity could reflect a taphonomic rather than a biological signal. Strombids have been present in the Indo-Pacific at least since the mid-Eocene, and present-day levels of strombid diversity were achieved by the Miocene.

Discussion

Pattern of Replacement.—Taxonomic, morphologic, and geographic data analyzed in this study all suggest the same pattern: gradual replacement of aporrhaids by strombids following the end-Cretaceous mass extinction.

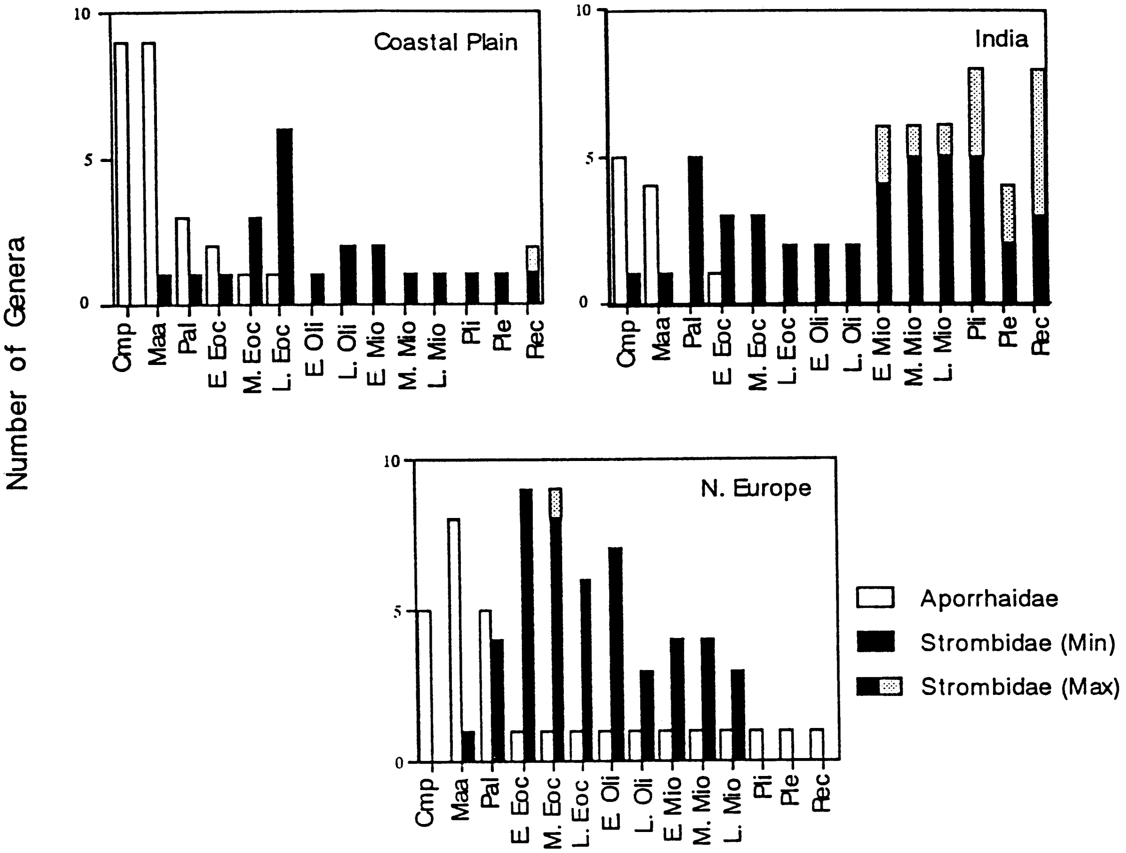

FIGURE 7. Patterns of replacement for individual geographic areas. Strombid diversity plotted using two different estimates (see text) with solid bars representing the minimum estimate and stippled bars the maximum. Open bars represent aporrhaid diversity. Note that while all the areas show a marked decrease in aporrhaid taxonomic diversity following the end-Maastrichtian extinction, the actual pattern of replacement varies among these areas (see text for a complete description and discussion).

Several aspects of this replacement need to be emphasized. First, from a taxonomic perspective, the highest rate of replacement was associated with a mass extinction, followed by a recovery of the aporrhaids (as evidenced by high origination rate) during the Paleocene, and the final phase of replacement during the Eocene (Figs. 1, 2). During these background times the taxonomic replacement was driven by higher originations in strombids rather than higher extinctions in aporrhaids (Fig. 2).

Second, the morphologic and geographic diversity patterns differ from the taxonomic pattern in that reciprocal trends, while present, are not strong. The major change in morphologic diversity for both groups was again associated with the end-Maastrichtian extinction event. The subsequent strombid taxonomic radiation was mostly confined to a relatively small segment of the morphospace (with the exception of *Lambis* and related genera; see Fig. 3). To the extent that morphology represents life habits (in this case, at least, there is reason to believe it does; see Savazzi 1991), I would argue that the morphologic patterns documented here largely reflect the successful, albeit rather specialized, ecological strategy of the strombids. Of course an alternative interpretation would be that the restriction in morphospace is due to phylogenetic and/or developmental constraints. This, however, seems unlikely as at least a few strombids (*Lambis, Millepes,* and *Harpago*) evolved a morphology that is highly convergent on some Mesozoic aporrhaid genera (e.g., *Harpagodes*). It is interesting that the escape response in Recent species of *Lambis* is different from most species of *Strombus* (Berg 1974) and resembles that of *Arrhoges occidentalis. Lambis, Millepes,* and *Harpago* also appear to have always been restricted to the Indo-Pacific and hence are different from most other strombids, which tend to have much broader geographic ranges.

Finally, the geographic data indicate a discordance between the patterns of replacement at a global vs. a local scale. The global geographic pattern is very similar to the taxonomic pattern in that the total number of geographic divisions occupied by the strombids increases through the Cenozoic while aporrhaids show a steady decline. During this time the geographic overlap (on a global scale) between the two groups also declines monotonically. At a smaller geographic scale, however, a more mosaic pattern of replacement is apparent. In the Indian subcontinent and Indo-Pacific, strombids appear to have replaced aporrhaids shortly after the end-Maastrichtian extinction. In the Coastal Plain the replacement was initiated by the extinction but was not completed until 20–30 m.y. later. In northern and southern Europe aporrhaid diversity showed a drastic reduction by the end-Cretaceous extinction, followed by a rapid strombid radiation during the Paleogene. Strombid diversity, however, decreased rapidly after the Paleogene and strombids finally became extinct in these areas by the Plio-Pleistocene, while one aporrhaid genus survived. The variations in these local patterns are probably due to the differences in prevailing climatic conditions (see below), again underscoring the point that patterns of replacement may look different at different scales of analysis (see Lidgard et al. 1993 for a similar argument regarding taxonomic diversity).

Thus, the replacement of aporrhaids by strombids involved (1) two groups, both characterized by a specialized set of antipredatory traits with one group being functionally superior, at least with respect to certain attributes; (2) a mass extinction event in which the diversity of the incumbents (aporrhaids) was significantly reduced, thereby diminishing the ecological advantages of incumbency; (3) postextinction replacement of the incumbent mediated by differential origination of strombid genera; and (4) complete geographic overlap of the interacting groups initially but progressive decrease in overlap as one group replaced the other. I interpret these patterns to support the notion that both mass extinction and biotic interactions were important in the replacement of aporrhaids by strombids.

The geographic data also highlight the importance of environmental parameters during replacement. As noted earlier, throughout their evolutionary history the strombids have been confined to tropical and subtropical areas, except during the Paleogene when they show high generic diversity in higher latitudes (e.g., Paris Basin, London Clay). A number of paleoclimatic reconstructions have suggested that near subtropical conditions prevailed in high latitudes during the early Eocene whereas the early Oligocene was characterized by significant cooling (see Zachos et al. 1993 and references therein). Thus the invasion and rapid radiation of strombids in mid-latitude areas during the early Eocene were probably triggered by the climate-mediated expansion of their preferred habitat into these regions. The effects of the Oligocene cooling event, on the other hand, appeared to have been more subtle as the strombids survived in northern Europe (although with very low diversity) till the end of the Miocene. Aporrhaids were moderately diverse in northern Europe during the Paleocene (a result of a rebound after the end-Cretaceous extinction) but were reduced to one genus by the early Eocene. Thus it seems that strombids did not just radiate in mid- to high-latitude areas during the Paleogene, they actually replaced aporrhaids in these areas. This has important implications from the replacement perspective. In modern oceans, temperate areas serve as refuges for the two surviving genera of aporrhaids. Similarly, in West Africa, where the two groups overlap, the strombid species occurs in shallow, warmer waters and the two aporrhaid species occur at cooler depths (Kronenberg 1991). It seems reasonable to postulate that the aporrhaid and strombid diversity patterns would probably be very different today if the Eocene climatic warming had not permitted a radiation of strombids into higher latitudes, thereby temporarily destroying a large segment of the aporrhaid refugia.

One issue that needs to be addressed here is whether the temperate strombid radiation and aporrhaid decline resulted from biotic interactions when the two groups were brought into contact by environmental change or whether they were simply a differential response to the same environmental change. As Benton (1987) has pointed out, if two groups respond in different (opposite) ways to an environmental change, then a "double-wedge" pattern could result even in the absence of any direct interaction between them. In the present case, biotic interaction seems more likely than differential environmental response for two reasons: (1) aporrhaids were present in tropical as well as temperate areas during the Mesozoic and early Cenozoic, and hence it seems unlikely that they would be adversely affected simply by a change from temperate to subtropical condition; and (2) the geographic data show that the "double-wedge" pattern was also present in lower latitudes where subtropical conditions presumably prevailed throughout (e.g., Coastal Plain, Indian subcontinent).

Biotic Interactions and Replacements.—Can biotic interaction be considered a dominant force in large-scale ecological replacements? While opinion still remains sharply divided on this issue, there is a growing body of evidence arguing in favor of an important role for such interactions. In fact, the lack of empirical evidence for past biotic interactions partly reflects methodological limitations; indeed interactions are extremely difficult to study even in Recent communities. That, however, does not justify the fact that, with a few exceptions, the whole paleobiological debate about biotic interactions has been based on inappropriate data, i.e., taxonomic diversity (see Vermeij 1987; Jackson 1988). Biotic effects may be important in large-scale replacements, but this fact can never be established solely with taxonomic diversity data, no matter how good. It is probably not accidental that the few recent studies that have examined other kinds of data (e.g., geographic, functional) in the context of replacements have inferred biotic interactions to be important (see Krause 1986; Maas et al. 1988; Rosenzweig and McCord 1991; Lidgard et al. 1993). The use of different types of data in conjunction will never prove the presence of interaction (or its absence for that matter) but could build a convincing case, which, as pointed out by Roughgarden (1984), may be all we are after anyway.

Biotic Replacements: What Have We Learned?—We still poorly understand the macroevolutionary processes underlying large-scale biotic replacements. Unfortunately, one major obstacle happens to be the lack of relevant empirical data that can be used to test various ideas about the replacement process. Conceptual arguments are important and new theoretical models linking ecology and macroevolution are definitely required, but these models can be tested only with the appropriate type of data from the fossil record. Taxonomic diversity data are important as they identify the instances of replacement, but such data are not sufficient to test different models of replacement. Biotic replacement is a complex phenomenon that almost certainly results from the interaction of a number of different forces (e.g., Krause 1986; Maas et al. 1988; Rosenzweig and McCord 1991; Lidgard et al. 1993). Results of the present study suggest that long-term biotic interactions, mass extinctions, and environmental changes during background times can all play important roles in the replacement process. The relative importance of each of these factors would, of course, vary from one replacement event to another. Thus the question that needs to be addressed (using theoretical models as well as relevant empirical data) is not whether all replacements are driven by biotic interactions, by mass extinctions, or by environmental change, but what is the relative importance of each of these factors in any given replacement event.

Acknowledgments

This paper grew out of discussions with D. Jablonski, M. LaBarbera, S. Lidgard, and J. J. Sepkoski, Jr. I thank D. H. Erwin, M. Foote, D. Jablonski, M. LaBarbera, A. I. Miller, M. L. Rosenzweig, J. J. Sepkoski, Jr., and G. J. Vermeij for extremely helpful comments on previous versions of the manuscript. Access to museum collections was provided by T. Waller, W. Blow, and F. Collier (National Museum of Natural History), N. J. Morris and R. Cleevely (Natural History Museum, London), Y. Gerard (Museum national d'Histoire Naturelle, Paris), L. R. Saul (Natural History Museum of Los Angeles County), W. J. Zinsmeister (Purdue University), D. T. Dockery III (Mississippi Department of Environmental Quality, Office of Geology), and S. K. Donovan (University of West Indies). N. F. Sohl made available the Cretaceous material housed at the U.S. Geological Survey, Reston. My thanks to all. Financial support for this study was provided by grants from the Geological Society of America, Sigma Xi, American Museum of Natural History (Theodore Roosevelt Memorial Fund), Hinds and Obering Funds (University of Chicago), and the National Science Foundation (grant EAR90-05744 to D. Jablonski).

Literature Cited

Abbott, R. T. 1960. The genus *Strombus* in the Indo-Pacific: Indo-Pacific Mollusca 1:33–146.

Allmon, W. D. 1994. Taxic evolutionary paleoecology and the ecological context of macroevolutionary change. Evolutionary Ecology 8:95–112.

Benton, M. J. 1987. Progress and competition in macroevolution. Biological Reviews of the Cambridge Philosophical Society 62:305–338.

———. 1991. Extinction, biotic replacements, and clade interactions. Pp. 89–102 *in* E. C. Dudley, ed. The unity of evolutionary biology. Dioscorides, Portland, Ore.

Berg, C. J., Jr. 1974. A comparative ethological study of strombid gastropods. Behaviour 51:274–322.

———. 1975. Behavior and ecology of conch (Superfamily Strombacea) in a deep subtidal algal plain. Bulletin of Marine Science 25:307–317.

Clench, W. J., and R. T. Abbott. 1941. The genus *Strombus* in the western Atlantic. Johnsonia 1:1–15.

Eldredge, N. 1985. Unfinished synthesis: biological hierarchies and modern evolutionary thought. Oxford University Press, New York.

———. 1986. Information, economics and evolution. Annual Review of Ecology and Systematics 17:351–369.

———. 1989. Macroevolutionary dynamics. Species, niches and adaptive peaks. McGraw Hill, New York.

———. 1992. Where the twain meet: causal intersections between the genealogical and ecological realms. Pp. 1–14, *in* N. Eldredge, ed. Systematics, ecology, and the biodiversity crisis. Columbia University Press, New York.

Erwin, D. H. 1990. Carboniferous–Triassic gastropod diversity patterns and the Permo-Triassic mass extinction. Paleobiology 16:187–203.

Foote, M. 1990. Nearest-neighbor analysis of trilobite morphospace. Systematic Zoology 39:371–382.

———. 1991a. 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.

———. 1991b. Analysis of morphological data. Pp. 59–86 *in* N. L. Gilinsky and P. W. Signor, eds. Analytical paleobiology. Short Courses in Paleontology, Number 4. Paleontological Society, Knoxville, Tenn.

———. 1992. Rarefaction analysis of morphological and taxonomic diversity. Paleobiology 18:1–16.

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

Geary, D. H., and W. D. Allmon. 1990. Biological and physical contributions to the accumulation of strombid gastropods in a Pliocene shell bed. Palaios 5:259–272.

Gould, S. J. 1989. Wonderful life: the Burgess Shale and the nature of history. W. W. Norton, New York.

———. 1991. The disparity of the Burgess Shale arthropod fauna and the limits of cladistic analysis: why we must strive to quantify morphospace. Paleobiology 17:411–423.

Gould, S. J., and C. B. Calloway. 1980. Clams and brachiopods—ships that pass in the night. Paleobiology 6:383–396.

Haefelfinger, R. 1968. Lokomotion von *Aporrhais pespelecani*. Revue Suisse de Zoologie 75:569–574.

Hallam, A. 1990. Biotic and abiotic factors in the evolution of early Mesozoic marine molluscs. Pp. 249–269 *in* Ross and Allmon 1990.

Hay, M. E. 1994. Species as "noise" in community ecology: do seaweeds block our view of the kelp forest? Trends in Ecology and Evolution 9:414–416.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annual Review of Ecology and Systematics 25:495–520.

Jablonski, D. 1989. The biology of mass extinction: a palaeontological view. Philosophical Transactions of the Royal Society of London B 325:357–368.

Jablonski, D., and D. J. Bottjer. 1990. Onshore-offshore trends in marine invertebrate evolution. Pp. 21–75 *in* Ross and Allmon 1990.

Jackson, J. B. C. 1988. Does ecology matter? Paleobiology 14: 307–312.

Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23:269–86.

Jung, P. 1974. A revision of the family Seraphsidae (Gastropoda: Strombacea). Palaeontographica Americana 8:5–69.

Koch, C. F. 1987. Prediction of sample size effects on the measured temporal and geographic distribution pattern of species. Paleobiology 13:100–107.

Koch, C. F., and N. F. Sohl. 1983. Preservational effects in paleoecological studies: Cretaceous mollusc examples. Paleobiology 9:26–34.

Krause, D. W. 1986. Competitive exclusion and taxonomic displacement in the fossil record: the case of rodents and multituberculates in North America. Pp. 95–117 *in* K. M. Flanagan and J. A. Lillegraven, eds. Vertebrates, phylogeny and philosophy. Contributions to Geology, Special Paper 3. The University of Wyoming, Laramie.

Kronenberg, G. C. 1991. The Recent species of the family Aporrhaidae. Vita Marina 41:73–84.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115–129.

Lidgard, S., F. K. McKinney, and P. D. Taylor. 1993. Competition, clade replacement, and a history of cyclostome and cheilostome bryozoan diversity. Paleobiology 19:352–371.

Maas, M. C., D. W. Krause, and S. G. Strait. 1988. The decline and extinction of Plesiadapiformes (Mammalia: ?Primates) in North America: displacement or replacement? Paleobiology 14:410–431.

Massot, M., J. Clobert, J. Lecomte, and R. Barbault. 1994. Incumbent advantage in common lizards and their colonizing ability. Journal of Animal Ecology 63:431–440.

Masters, J. C., and R. J. Rayner. 1993. Competition and macroevolution: the ghost of competition yet to come? Biological Journal of the Linnean Society 49: 87–98.

Merz, R. A. 1979. A study of the behavioral and biomechanical defenses of *Strombus alatus*, the Florida fighting conch. Master's thesis. University of Florida, Gainesville.

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

Percharde, P. L. 1968. Notes on distribution and underwater observations of the molluscan genus *Strombus* as found in the waters of Trinidad and Tobago. Caribbean Journal of Science 8:47–53.

———. 1970. Further underwater observations on the molluscan genus *Strombus* as found in the waters of Trinidad and Tobago. Caribbean Journal of Science 10:73–81.

Perron, F. E. 1978a. Seasonal burrowing behavior and ecology of *Aporrhais occidentalis* (Gastropoda: Strombacea). Biological Bulletin 154:463–471.

———. 1978b. Locomotion and shell-righting behaviour in adult and juvenile *Aporrhais occidentalis* (Gastropoda: Strombacea). Animal Behaviour 26:1023–1028.

Pimm, S. L. 1991. The balance of nature? University of Chicago Press, Chicago.

Raup, D. M. 1979. Biases in the fossil record of species and genera. Carnegie Museum of Natural History Bulletin 13:85–91.

———. 1991. The future of analytical paleobiology. Pp. 207–216 *in* N. L. Gilinsky and P. W. Signor, eds. Analytical paleobiology. Short Courses in Paleontology, Number 4. Paleontological Society, Knoxville, Tenn.

Raup, D. M., S. J. Gould, T. J. M. Schopf, and D. S. Simberloff. 1973. Stochastic models of phylogeny and the evolution of diversity. Journal of Geology 81:525–542.

Rosenzweig, M. L., and R. D. McCord. 1991. Incumbent replacement: evidence for long term evolutionary progress. Paleobiology 17:202–213.

Ross, R. M., and W. D. Allmon. 1990. Causes of evolution: a paleontological perspective. University of Chicago Press, Chicago.

Roughgarden, J. 1984. Competition and theory in community ecology. Pp. 3–21 *in* G. W. Salt, ed. Ecology and evolutionary biology: a roundtable of research. University of Chicago Press, Chicago.

Roy, K. 1994. Effects of the Mesozoic Marine Revolution on the taxonomic, morphologic and biogeographic evolution of a group: aporrhaid gastropods during the Mesozoic. Paleobiology 20:274–296.

Runnegar, B. 1987. Rates and modes of evolution in the Mollusca. Pp. 39–60 *in* K. S. W. Campbell and M. F. Day, eds. Rates of evolution. Allen and Unwin, London.

Savazzi, E. 1991. Constructional morphology of strombid gastropods. Lethaia 24:311–331.

Sepkoski, J. J., Jr. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinction. Paleobiology 10:246–267.

———. 1987. Reply to Patterson and Smith. Nature 330:252.

———. 1994. The double wedge revisited: how should competitive displacement look? Geological Society of America Abstracts with Programs 26:A175.

Sepkoski, J. J., Jr., and D. C. Kendrick. 1993. Numerical experiments with model monophyletic and paraphyletic taxa. Paleobiology 19:168–184.

Smith, A. B. 1994. Systematics and the fossil record. Blackwell Scientific, Oxford.

Smith, A. B., and C. Patterson. 1988. The influence of taxonomic method on the perception of patterns of evolution. Evolutionary Biology 23:127–216.

Stanley, S. M. 1979. Macroevolution: pattern and process. W. H. Freeman, San Francisco.

Stanley, S. M., and W. A. Newman. 1980. Competitive exclusion in evolutionary time: the case of the acorn barnacles. Paleobiology 6:173–183.

Valentine, J. W. 1990. The macroevolution of clade shape. Pp. 128–150 *in* Ross and Allmon 1990.

Van Valen, L. 1985. A theory of origination and extinction. Evolutionary Theory 7:133–142.

———. 1994. Concepts and the nature of selection by extinction: is generalization possible? Pp. 200–216 *in* W. Glen, ed. Mass-extinction debates: how science works in a crisis. Stanford University Press, Stanford, Calif.

Vermeij, G. J. 1987. Evolution and escalation, an ecological history of life. Princeton University Press, Princeton, N.J.

———. 1994. The evolutionary interaction among species: selection, escalation and coevolution. Annual Review of Ecology and Systematics 25:219–36.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Williams, G. C. 1992. Natural selection: domains, levels, and challenges. Oxford University Press, New York and Oxford.

Zachos, J. C., K. C. Lohmann, J. C. G. Walker, and S. W. Wise. 1993. Abrupt climate change and transient climates during the Paleogene: a marine perspective. Journal of Geology 101: 191–213.