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Effects of the Mesozoic Marine Revolution on the taxonomic, morphologic, and biogeographic evolution of a group: aporrhaid gastropods during the Mesozoic

Kaustuv Roy

Abstract.—The mid-Mesozoic time was characterized by massive reorganization of the ecological structure of benthic marine communities. Although the general pattern of this "Mesozoic Marine Revolution" has been extensively documented, little is known about how it affected the taxonomic and morphologic diversities of individual lineages of organisms. Here I document group-level dynamics of the Mesozoic change using the fossil record of aporrhaid gastropods, a diverse and widespread family during that time. Using data gathered through field and museum work and extensive literature search, I compare and contrast patterns of taxonomic and morphologic change during the Jurassic and Cretaceous within a geographic framework. I also examine how the changes were manifested at different ecological and geographic scales.

The Mesozoic history of the Aporrhaidae includes two major radiations separated by a period of overall stability. While both radiations increased the taxonomic diversity of the family, they had very different morphologic consequences, resulting in a striking discordance between morphologic and taxonomic diversity patterns. The initial radiation during Bajocian–Bathonian times established two large morphologic groups within the aporrhaids based mainly on differences in the shape of the apertural margin. The second, post-Albian, radiation saw higher origination rates and increased taxonomic and morphologic diversity among genera having simpler apertural margins, while genera with elaborate multidigitate apertures declined in taxonomic diversity but not in morphologic diversity. During post-Albian times the group with simpler apertural margins also tended to be more widespread compared to the group with multidigitate apertures. Comparison of regional and global taxonomic diversities reveals a discordance between regional and global taxonomic patterns: while diversities within certain geographic areas increased in concert with the global radiation, those for other areas decreased substantially, resulting in a remarkably constant average taxonomic diversity within geographic areas.

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Introduction

One of the most significant changes in the ecological structure of benthic marine communities began during the mid-Mesozoic. This reorganization, termed the "Mesozoic Marine Revolution," included a number of important events such as the diversification of major groups of durophagous predators and predatory mollusks, significant increase in repaired shell damage among gastropods, increase in antipredatory morphologies in various molluscan groups, disappearance of stalked crinoids and brachiopods from shallow-water habitats, and a substantial increase in levels of bioturbation (Meyer and Macurda 1977; Vermeij 1977, 1983, 1987; Steneck 1983; Thayer 1983; Lidgard et al. 1993).

Although the general pattern of change is clear, little is known about the dynamics of the Mesozoic Revolution at the level of individual clades or within individual geographic regions. The lack of such data has prevented a better understanding of the nature of this change and the underlying processes. In fact, the few studies that have attempted to document this change for individual groups suggest that effects can be highly clade-specific. For example, Budd and Coates (1992) examined the morphologic changes exhibited by *Montastraea*-like corals during the Cretaceous, but failed to detect any long-term evolutionary trends. Ward (1986), on the other hand, documented important temporal changes in shell morphology of various groups of ammonoids during the same time period.

While most studies of the Mesozoic Revo-

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lution have documented temporal patterns of either taxonomic or morphologic change for various groups of marine organisms, almost none has explicitly attempted to compare and contrast these two types of patterns. Recent work has shown that a comparison of temporal patterns of taxonomic and morphologic diversity of a group can often provide insights into the macroevolutionary processes underlying the changes (see Foote 1993). Hence, such a comparative approach, especially in a geographic context, should greatly aid in understanding the dynamics of the Mesozoic change. Similarly, attempts to examine the nature of the Mesozoic change at different ecological and geographic scales have been lacking despite the observation that a comparison of patterns at different ecological levels can provide important information about evolutionary radiations (Bambach 1977; Sepkoski 1988; Lidgard et al. 1993).

In this paper, I examine the clade-level dynamics of the Mesozoic Marine Revolution using a multifaceted approach. I first document global patterns of taxonomic and morphologic diversity exhibited by Jurassic and Cretaceous genera of aporrhaid gastropods, a group that was an important component of the shallow-water molluscan fauna during the Mesozoic Revolution. I then document the patterns of geographic distribution exhibited by the Mesozoic aporrhaids and use this geographic framework to (1) compare and contrast the temporal patterns of taxonomic and morphologic diversity, and (2) examine temporal patterns of taxonomic diversity at a global as well as a local scale. In addition, I use the preliminary results from a cladistic analysis of the Jurassic aporrhaid genera to discuss the phylogenetic aspects of the morphologic radiations documented here.

The Group

Ecology.—The gastropods of the family Aporrhaidae are characterized by a highly modified and expanded apertural margin and exhibit some of the most striking morphologies known in any gastropod group, fossil or Recent (fig. 1). Aporrhaid gastropods show determinate growth in which the apertural modifications are produced only after growth has ceased and the animal has attained sexual maturity. Although the functional significance of the apertural modifications is poorly understood, it is clear that the ontogenetic change in aporrhaid shell morphology has several important consequences including significant differences in the mode of locomotion between adults and juveniles (see Perron 1978b for a description). As far as life habit is concerned, juvenile aporrhaids tend to be largely infaunal while the adults are seasonal burrowers (Perron 1978a on *Arrhoges occidentalis*; Barnes and Bagenal 1952 on *Aporrhais pespelecani*). Adult individuals of *Arrhoges occidentalis* remain epifaunal for part of the year during which time they graze on benthic diatoms and decaying macroalgae (Perron 1978a). The rest of the year is spent inside the sediment. Interestingly enough, stomach content analyses indicate seasonal changes in feeding behavior associated with burrowing (Perron 1978a). During the infaunal stage the animals have empty stomachs and intestines and appear to lack a crystalline style in the style sac. While seasonal burrowing behavior appears to be characteristic of aporrhaids (and stromboidean gastropods in general), its role in the life history of these organisms remains poorly understood at present (Perron 1978a).

Phylogenetic Relationships.—As discussed below, the aporrhaids originated during the Late Triassic, reached maximum taxonomic diversity and a global distribution in the Late Cretaceous, suffered heavily during the end-Cretaceous extinction, and declined in diversity throughout the Cenozoic. From a phylogenetic perspective there are two main hypotheses regarding the ancestry of aporrhaids. Traditionally aporrhaids were thought to be closely related to the Cerithidae (see e.g., Gardner 1875), whereas Bandel (1991) suggested that they evolved from the Triassic group Loxonematoidea. Bandel's hypothesis, however, is based strictly on the apparent morphological similarity of larval shells of certain members of the two groups and is yet to be tested using other characters. Thus, further phylogenetic information is needed to resolve the question about the ancestry of aporrhaids.

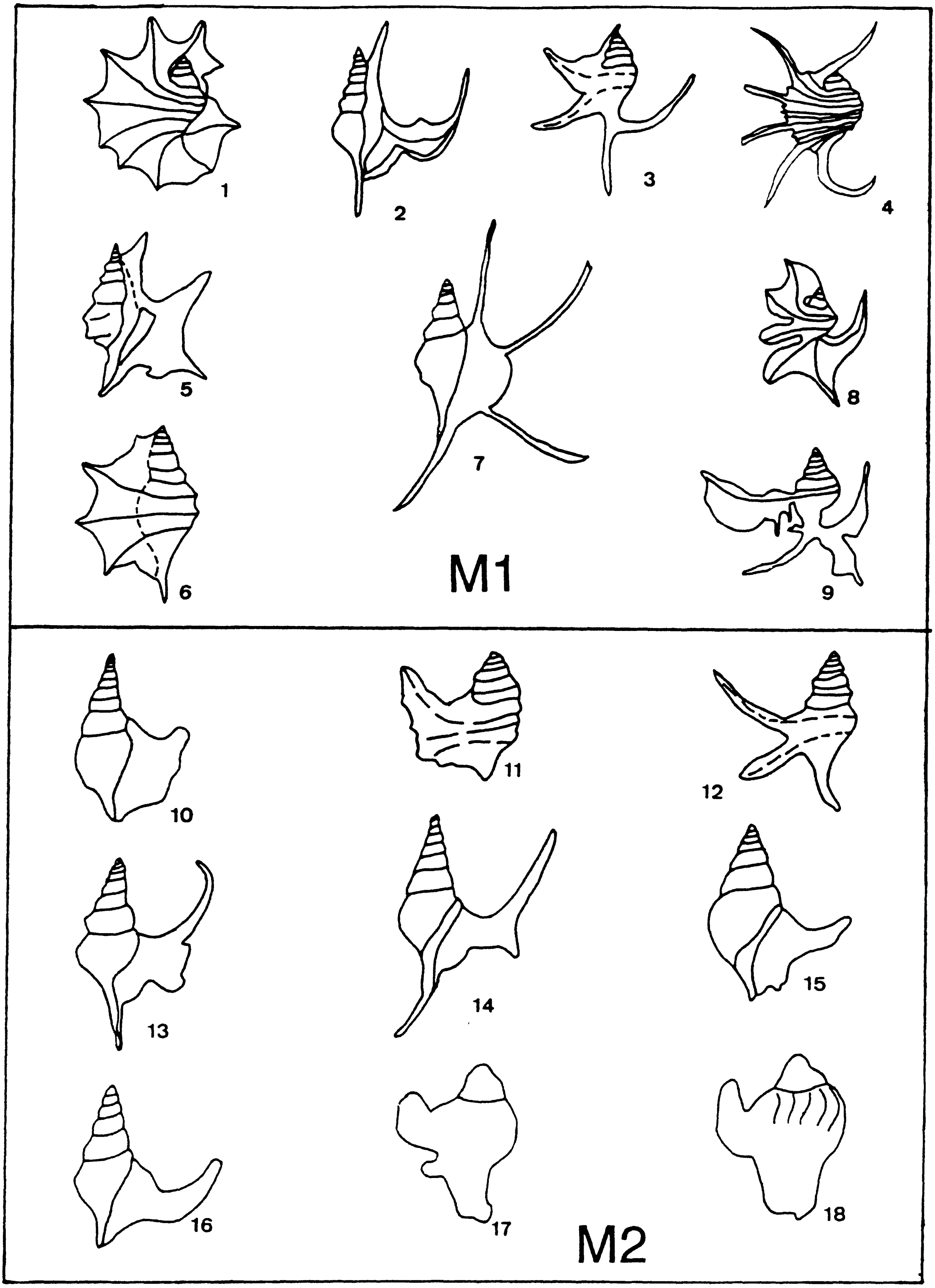

FIGURE 1. Morphologies of selected aporrhaid genera. The line drawings are based on Wenz (1943), Sohl (1960), and photographs of various museum specimens. Drawings not to scale. 1–9 are characterized by multidigitate

The aporrhaids are generally considered to be ancestral to two Cenozoic gastropod families, the Strombidae and the Struthiolariidae. Thus, the family Aporrhaidae is paraphyletic. However, since the strombids and struthiolariids were neither abundant nor diverse during the Jurassic and Cretaceous, the exclusion of a handful of species and available specimens is unlikely to affect the long-term morphologic patterns documented here. In fact, the Cenozoic decline of the aporrhaids appears to have been the result of gradual replacement by the strombids (Roy 1992). Secondly, the Cretaceous strombids and struthiolariids were characterized by simple apertural margins and hence their inclusion would only strengthen the morphological patterns documented here. Finally, while all stromboidean gastropods share certain basic ecological characteristics, the aporrhaids have certain unique functional traits (e.g., mode of locomotion) that make them ecologically distinct from the strombids and the struthiolariids (in addition to the discussion above, see Berg [1974] for ethology of stromboidean gastropods; Perron [1978a], Barnes and Bagenal [1952], and Yonge [1937] for ecology of aporrhaids; and Geary and Allmon [1990], and Savazzi [1991] for a review of the ecology of strombids).

Methods

The data for this analysis came from three principal sources: (1) field collections from the Upper Cretaceous Coffee Sand of Mississippi, Fox Hills Formation and Pierre Shale of South Dakota and Montana, and Guinea Corn Formation of Jamaica; (2) 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; British Geological Survey; Muséum National d'Histoire Naturelle, Paris; Department of Earth and Atmospheric Sciences, Purdue University; and the Museum of the University of West Indies, Mona, Kingston, Jamaica; and (3) an extensive literature search (see below).

Taxonomic Diversity.—Data on taxonomic diversity were compiled from all three of the above sources, focusing at the generic level. The taxonomic scheme for the Aporrhaidae used by Cossmann (1903) and Wenz (1943) recognized ten genera that were subdivided into a number of subgenera. Current workers generally treat Wenz's subgenera as genera because they represent discrete species groups (see Sohl 1960). Due to the extreme morphologic plasticity exhibited by most aporrhaid species (including the extant ones), fossil species are difficult to define objectively and, as pointed out by Sohl (1960), many existing species names are undoubtedly synonyms. An additional problem is the introduction, especially by early workers (e.g., d'Orbigny 1842), of a large number of specific names for indeterminate aporrhaid steinkerns which must be treated as *nomen dubia.*

In this study I have used a taxonomic scheme that divides the aporrhaids into 36 genera (see Appendix 1), each of which represents a distinct type of apertural morphology. In compiling taxonomic diversity, I have only included published and museum specimens that were sufficiently well preserved for me to assign them to one of these 36 genera. In cases where my assignments differed from the original author's, I have used the revised assignments to calculate taxonomic diversity. Although this approach led to the exclusion of a number of early records, it was necessary in order to achieve an acceptable level of taxonomic uniformity for the group.

For the purpose of this study, taxonomic diversity is defined as the number of genera present during any given time interval. The time intervals used here are the standard stages for Jurassic and Cretaceous (Harland et al. 1990) except that I combined the Tu-

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apertures and belong to the morphologic group M1 while 10–18 have simpler apertures and belong to M2. The genera are: 1. *Phyllocheilus;* 2. *Helicaulax;* 3. *Tessarolax;* 4. *Harpagodes;* 5. *Aporrhais;* 6. *Quadrinervus;* 7. *Cuphosolenus;* 8. *Pterocerella;* 9. *Tridactylus;* 10. *Arrhoges;* 11. *Monocuphus;* 12. *Dicroloma;* 13. *Perissoptera;* 14. *Anchura;* 15. *Graciliala;* 16. *Drepanochilus;* 17. *Gymnarus;* 18. *Pugnellus.*

ronian, Coniacian, and Santonian stages in order to create an interval roughly comparable in duration to the other Cretaceous stages. The taxonomic origination and extinction rates, as calculated here, are per taxon rates calculated per million years. The error bars on these rates were calculated by estimating the standard error on percent extinction for individual stages by summing binomial probabilities (see Raup 1991; Raup and Jablonski 1993) and then dividing the error estimates by the respective stage durations; because there is unaccounted error in stage durations, the error bars represent minimum estimates of the true standard error.

From an ecological perspective, global taxonomic diversity consists of three major components: alpha diversity (diversity within a single community), beta diversity (taxonomic differentiation between communities), and gamma diversity (taxonomic differentiation between geographic regions) (Whittaker 1960, 1972, 1975; Cody 1975; Bambach 1977; Brown and Gibson 1983; Sepkoski 1988). Very few paleobiological studies have examined taxonomic diversities at different ecological scales in the context of global diversification of entire faunas. Exceptions include the seminal studies of Paleozoic radiations by Bambach (1977) and Sepkoski (1988). Lidgard et al. (1993) have recently used the same approach at the level of individual clades and demonstrated that it can provide important insight into the ecological and evolutionary dynamics of the group being studied. Lidgard et al. (1993) examined the post-Paleozoic decline of the cyclostome bryozoans and the corresponding radiation of the cheilostome bryozoans and concluded that the dynamics of the bryozoan clade replacement was manifested differently at different ecological levels. Accordingly, I have compiled taxonomic data of aporrhaid genera not only at the global level, but also within individual geographic areas to examine (1) patterns of temporal change in diversity within individual areas, and (2) variations in the temporal pattern of taxonomic differentiation of aporrhaids among geographic areas.

Morphologic Diversity.—In a series of recent papers, Foote (1990, 1991a,b, 1992, 1993) has discussed different ways in which morphologic diversity can be measured and their implications. At present there is no single, standard definition of morphologic diversity (Foote 1991a), and hence different metrics have been proposed by different workers (see, among others, Runnegar 1987; Gould 1989, 1991; Erwin 1990; Foote 1991a,b, 1993). Because the focus of this study is on temporal patterns of morphologic change, I have used 25 discrete binary characters (table 1) to construct a morphospace for 33 genera of aporrhaids and have examined how that morphospace was differentially filled through time. The characters used here (table 1) represent major morphologic themes that characterize aporrhaid genera. Hence, the changes in morphospace occupation represent basic changes in the morphological partitioning rather than smaller shifts associated with individual speciation events. For most of the genera, the characters were coded by examining specimens in museum collections. For the few genera where actual specimens were not examined, the character coding was based on reliable illustrations. Three genera, *Strombopugnellus, Tundora* and *Kangilioptera,* were excluded from the morphologic analysis due to insufficient information.

The temporal pattern of morphospace occupation was quantified using Q-mode nonmetric multidimensional scaling (MDS). Multidimensional scaling is a gradient analysis technique that reduces multidimensional data to a few dimensions (usually 2 to 4) in such a way that the distances among the low dimensional coordinates represent, as closely as possible, monotonic functions of the distances between the taxa (Marcus 1990). This makes the method especially attractive for matrices that are based on discrete characters. Despite its obvious attractions, this technique has not been widely used in the analysis of morphologic gradients and remains primarily a tool for ecologists and paleoecologists (see e.g., Gauch 1982; Kammer and Ausich 1987). I first generated a matrix of simple matching coefficients for the 33 genera using the 25 binary characters and then scaled it in three dimensions using the MDS routine in Systat 5.1 (Systat, Inc., Evanston, Ill.). The scores on the three dimensions were sorted stratigraphically using the ranges of individ-

TABLE 1. List of morphologic characters used to define aporrhaid morphospace.

1. Relative spire height: high, low (<half length of body whorl).
2. Sides of whorls: angular, round.
3. Shape of aperture: slit-like, semicircular.
4. Length of anterior process: long, short (<half length of body whorl).
5. Nature of anterior process: straight, curved.
6. Length of posterior canal: long, short/absent.
7. Spiral body chords extending to apertural process: present, absent.
8. Callus on spire: present, absent.
9. Posterior process adnate to spire: present, absent.
10. Posterior process extending beyond spire: present, absent.
11. Apertural callus: present, absent.
12. Spines on body: present, absent.
13. Spines on spire: present, absent.
14. Width of anterior process: narrow, broad.
15. Length of apertural digits: long, short.
16. Apertural expansion: wide, narrow.
17. Thin webb between apertural digits: present, absent
18. Concave posterior margin of wing: present, absent.
19. Digits extending around body whorl: present, absent.
20. Curvature of digits perpendicular to apertural plane: strong, weak.
21. Nature of apertural expansion: single, multidigitate.
22. Number of digits: 1-2, >2.
23. Sculpture: single type, ornate (both axial and spiral).
24. Thick webb between digits: present, absent.
25. Type of apertural process (lobed or spiny): single type, both.

ual genera and plotted for each time period to define the major morphologic groups. These sorted scores were also used to calculate morphologic diversities for individual time slices. Here I have expressed morphologic diversity as the geometric mean of the ranges of the ordination scores (Foote 1991a,b). As pointed out by Foote (1991b), this is the notion of morphologic diversity that is commonly used in paleobiologic studies (although not always quantitatively). Although intuitively reasonable, one apparent problem with this metric is that it is often positively correlated with sample size and hence, in some cases, it may be desirable to make necessary corrections (Foote 1991b, 1992). This, however, is not a problem in the present study as (1) the focus of this study is on fundamental changes in morphologic partitioning rather than on smaller shifts associated with individual speciation events and hence it is reasonable to assume that the observed range of morphotypes is a good approximation of the true range, and (2) the results of the morphologic analysis (see below) show that, for the aporrhaids, higher taxonomic diversity is often associated with lower morphologic diversity.

Biogeographic Patterns.—As pointed out by Koch and Sohl (1983) and Koch (1987), analyses of the geographic distribution of fossil taxa are particularly vulnerable to sampling problems. For aporrhaids, the biogeographic record is especially biased during the early radiation of the group (due to the extremely uneven global distribution of Jurassic and earliest Cretaceous marine sediments). To minimize sampling problems, the global data base was divided into 23 geographic divi-

TABLE 2. List of geographic divisions used in this study.

1. Gulf and Atlantic coastal plain
2. California, Oregon, Washington
3. India, Pakistan
4. North Africa & Arabia
5. West Africa
6. East Africa
7. South Africa
8. Northern Europe
9. Southern Europe
10. Central Europe
11. Western South America
12. Caribbean
13. Crimea, Caucasus, Soviet Central Asia
14. Western Interior of U.S.A.
15. Greenland
16. China, Tibet
17. Madagascar
18. Brazil and Venezuela
19. Antarctica
20. Australia, New Zealand
21. Japan
22. Indo Pacific

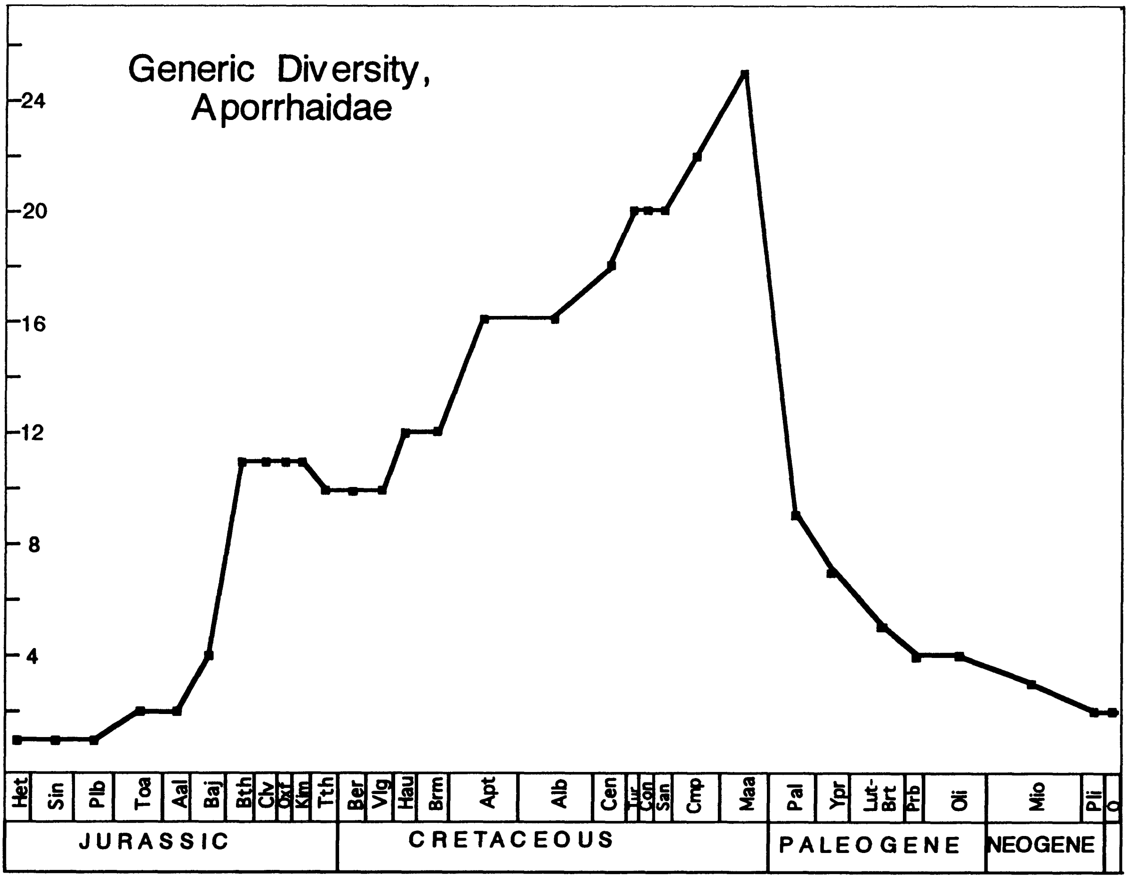

FIGURE 2. Generic diversity of aporrhaid gastropods from lower Jurassic to Recent, using the time scale of Harland et al. (1990). Diversities have been plotted at the midpoints of individual stages.

sions, thereby grouping data over large areas and multiple facies, and all biogeographic analyses were carried out using this rather coarse framework (table 2). It should be pointed out that while some of the geographic divisions used here correspond to recognized biogeographic entities (e.g., western interior), most represent strictly geopolitical units. To reduce the temporal unevenness of the data points further, the geographic distribution for each genus was derived by interpolating between the closest points representing its known stratigraphic distribution within each geographic division. This assumes that an absence between two known presences of a genus in the geological record of any given area is taphonomic and not due to emigration or environmental exclusion. Given the poor quality of the record (especially during the Jurassic and the Early Cretaceous), and the lack of any information indicating large-scale emigration, in the present situation a taphonomic explanation appears more reasonable than exclusion by facies or climatic changes.

Results

Taxonomic Diversity.—In general, the Mesozoic history of aporrhaid gastropods is characterized by two major radiations with an interim period of overall stability (fig. 2). The aporrhaids first appeared during the Late Triassic and began radiating during the Middle Jurassic, giving rise to at least 12 genera by the end of Bathonian. This was followed by a period (Callovian–Albian) of apparent stability, with a second radiation beginning in the Cenomanian and continuing through the Maastrichtian. The diversity of the group was severely reduced by the Maastrichtian mass extinction and, although there was a modest rebound during the Paleocene (figs.

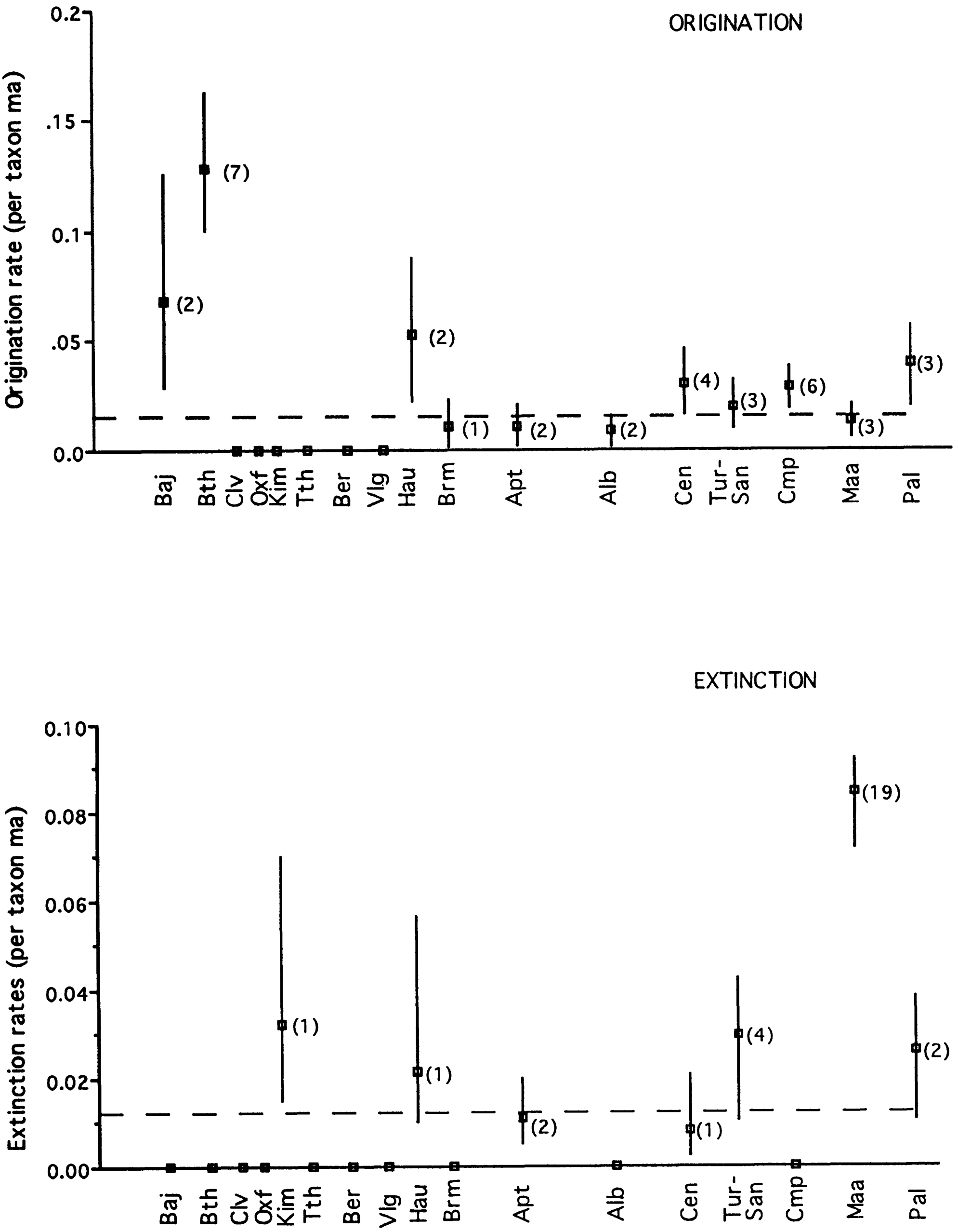

FIGURE 3. Origination and extinction rates of aporrhaid genera from mid-Jurassic to Paleocene. The rates are per-taxon rates calculated per million years. The numbers in parenthesis represent the actual number of originations or extinctions respectively. The error bars have been calculated following Raup (1991). The dashed lines represent the average origination and extinction rates respectively.

2, 3), diversity declined steadily throughout the rest of the Cenozoic. The present diversity of two genera was attained during the Pliocene.

The origination and extinction rates for the aporrhaids do not show any consistent temporal trends (fig. 3). In general, the Jurassic and earliest Cretaceous were characterized by few originations, interspersed with episodic bursts of high origination rates. During the rest of the Cretaceous, when diversity was higher, origination rates were more uniform, fluctuating around the mean (fig. 3).

In contrast to the global diversity pattern,

TABLE 3. Temporal patterns of taxonomic richness (number of genera) of aporrhaid gastropods within individual geographic divisions. Only divisions with non-zero diversity values are included.

Area	Paleocene	Campanian-Maastrichtian	Cenomanian-Santonian	Aptian-Albian
Coastal Plain*	3	13	7	6
N. Africa	1	5	7	5
N. Europe	4	12	13	14
S. Europe	1	2	6	9
C. Europe	2	1	6	2
Crimea	4	3	5	3
W. Interior*	1	6	4	1
Antarctica	1	2	1	3
Australia*	3	4	2	1
Japan	1	3	5	4
U.S. Pacific Coast*	2	8	5	3
Mean	2.09 ± 0.37	5.36 ± 1.22	5.54 ± 0.94	4.64 ± 1.17

* Divisions marked with asterisk show increasing taxonomic richness from Aptian to Maastrichtian.

the average standing diversity of aporrhaids within each geographic division remained roughly constant from the Aptian to the Maastrichtian with a marked drop following the end-Maastrichtian extinction (table 3). The average taxonomic differentiation between the geographic divisions (calculated using the Jaccard coefficient, Appendix 2), (see Sepkoski 1988; Whittaker 1972), also remained virtually constant during this period. This, of course, does not mean that there were no changes in standing diversity within each geographic area but simply that increases in diversity in some areas were balanced by decreases in others (table 3).

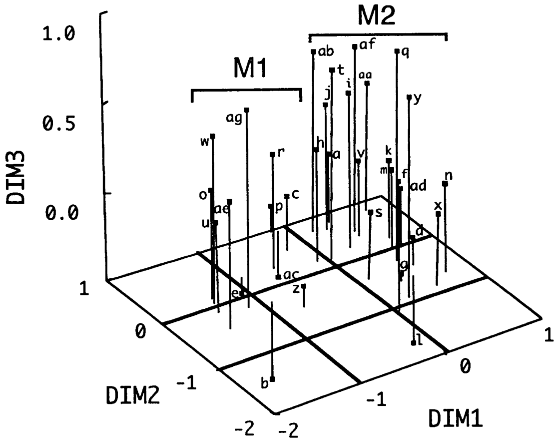

FIGURE 4. Position of various aporrhaid genera in the three dimensional morphospace defined by non-metric MDS. The group M1 consists of genera with elaborate multidigitate apertural margins whereas M2 consists of genera with simpler apertures. The genera are as follows: a. *Anchura*; b. *Aporrhais*; c. *Araeodactylus*; d. *Arrhoges*; e. *Cuphosolenus*; f. *Cuphotifer*; g. *Diarthema*; h. *Dicroloma*; i. *Diempterus*; j. *"Dimorphosoma"*; k. *Drepanochilus*; l. *Goniocheila*; m. *Graciliala*; n. *Gymnarus*; o. *Harpagodes*; p. *Helicaulax*; q. *Lispodesthes*; r. *Maussenetia*; s. *Monocuphus*; t. *Perissoptera*; u. *Phyllocheilus*; v. *Pietteia*; w. *Pterocerella*; x. *Pugnellus*; y. *Pyktes*; z. *Quadrinervus*; aa. *Spinigera*; ab. *Struthiochenopus*; ac. *Teneposita*; ad. *Tephlon*; ae. *Tessarolax*; af. *Tibiaporrhais*; ag. *Tridactylus*.

Morphologic Patterns.—As shown in figure 4, the aporrhaid genera fall into two broad morphologic groups, here designated M1 and M2, along the MDS axes. The Shepard plot for the three-dimensional MDS was linear and the stress of the final configuration was 0.094, indicating fairly low levels of distortion. The genera belonging to M1 are characterized, in general, by large, multidigitate apertural margins and exhibit negative scores on the first ordination axis, while those belonging to M2 typically exhibit simpler apertures and exhibit largely positive scores on the first axis (fig. 4). When the genera are sorted stratigraphically (figs. 5–7), it is apparent that: (1) the two morphologic groups were established fairly early in the history of aporrhaids; and (2) both groups show stable patterns of morphospace occupation throughout the Jurassic and earliest Cretaceous; however, (3) beginning in the Albian and continuing throughout the rest of the Cretaceous, new taxa were added preferentially to M2. Thus, by the end of the Cretaceous, M2 was more taxon-rich than M1 (table 4; fig. 7). Surprisingly, however, during the modest rebound immediately after the end-Cretaceous extinction, the two new Paleocene genera were both characterized by multidigitate apertural margins (i.e., belonged to M1, fig. 7). These new genera

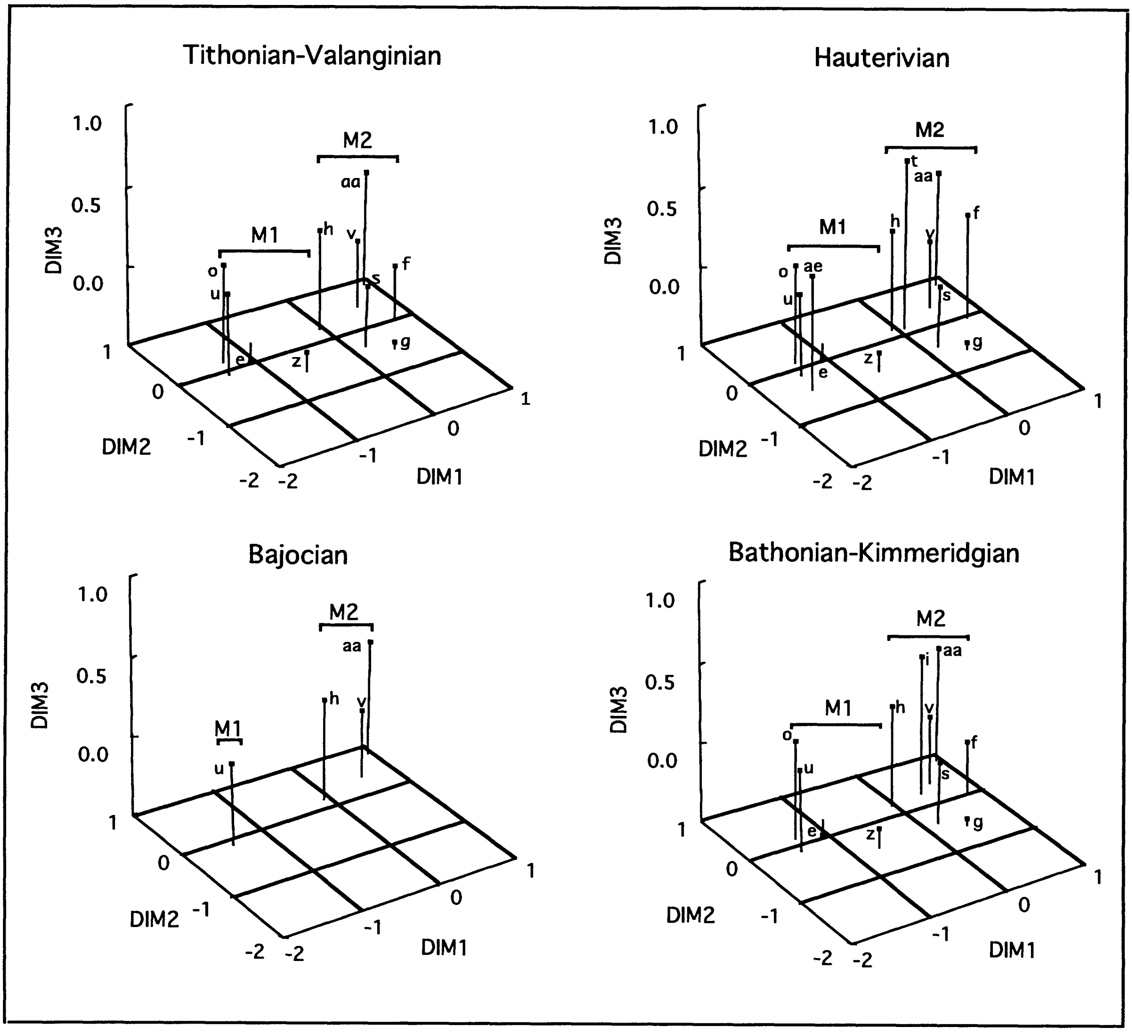

FIGURE 5. Temporal pattern of morphospace occupation of aporrhaid genera from mid-Jurassic to Lower Cretaceous. Abbreviations as in figure 4. Note that the two morphologic groups were established early and exhibit similar taxonomic diversities during this period.

were, however, rather short-lived and of the two extant genera, one (*Aporrhais*) is characterized by multidigitate apertural margin while the other (*Arrhoges*) has a simpler aperture.

In general, the taxonomic diversity of aporrhaids increased in concert with morphologic diversity during the Jurassic and Cretaceous radiations. This is true for the total diversity of the family as well as for the morphologic group M2 (table 4). For the M1 genera morphologic diversity increased along with taxonomic diversity from Bajocian to Santonian times. However, the post-Santonian decline in the taxonomic diversity of this group was accompanied not by a similar decrease in morphologic diversity but instead by a slight increase (table 4).

Comparison of morphologic and taxonomic diversities of the groups M1 and M2 reveal some interesting patterns. Before the Aptian, the morphologic group M2 was slightly more diverse than M1 both taxonomically and morphologically. However, the Cretaceous radiation gave rise to a discordance between the taxonomic and morphologic patterns. During this time M2 became substantially more taxon-rich compared to M1, but M1 had higher

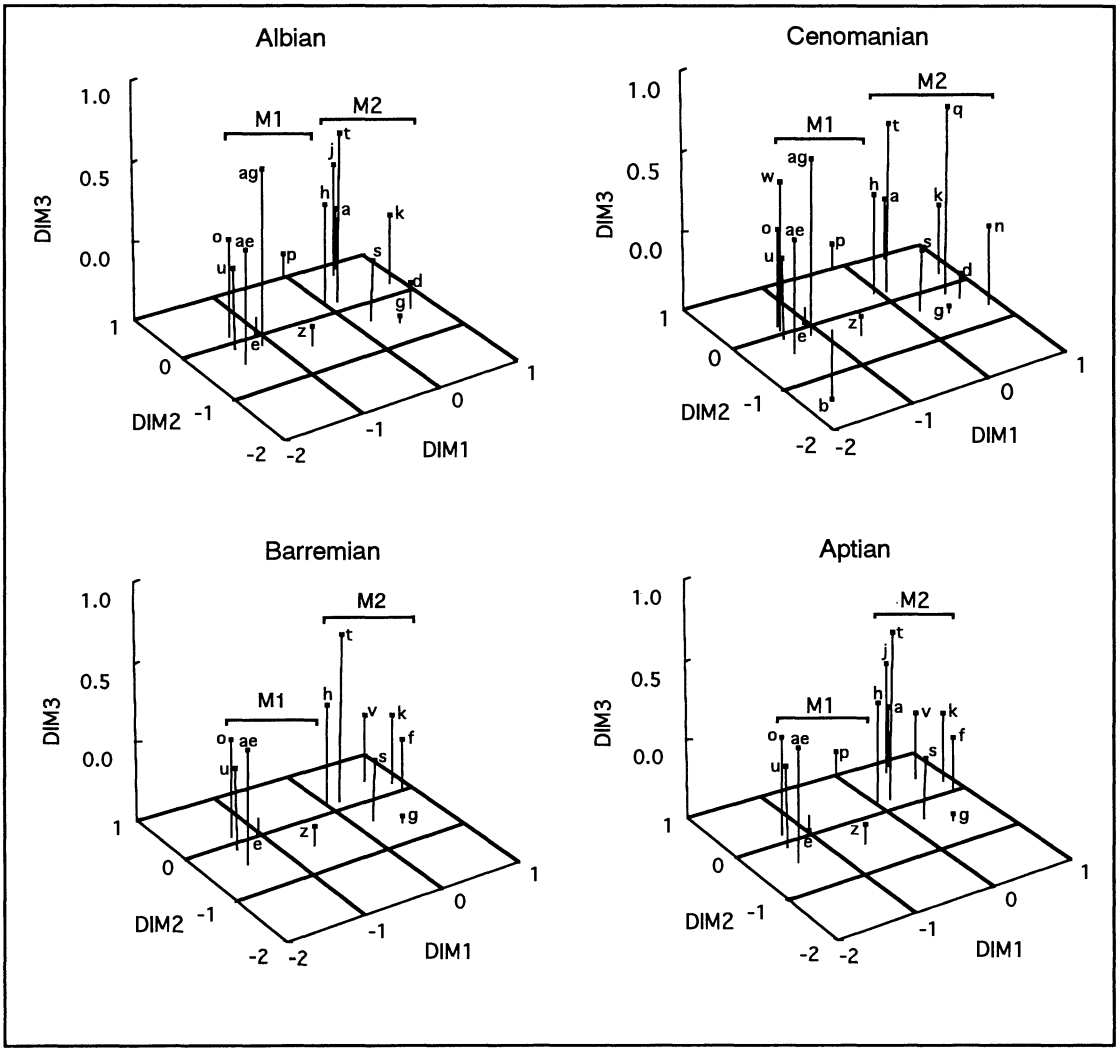

FIGURE 6. Temporal pattern of morphospace occupation of aporrhaid genera during the mid-Cretaceous. Abbreviations as in figure 4. Note that both morphologic groups were diversifying during this time and exhibit comparable taxonomic diversities.

morphologic diversity. This higher morphologic diversity for M1 was maintained even in the face of a 2:1 disparity in taxonomic richness during the Maastrichtian. The extinction event at the end of the Maastrichtian severely reduced the taxonomic diversity of aporrhaids but did not affect their morphologic diversity to the same extent (table 4).

The discordance between the patterns of taxonomic and morphologic diversity described above is comparable to patterns recently documented for other clades (e.g., Blastoidea, Trilobita, Libristoma, and Asaphina; see Foote 1993), where high levels of morphologic diversity were maintained even in the face of severe reductions in taxonomic richness. While the question about the frequency of these discrepancies remains yet to be settled (Foote 1993), the present study provides a Mesozoic example of a pattern that has been mostly documented in Paleozoic clades.

Biogeographic Patterns.—Biogeographic frequency distributions (i.e., the number of geographic divisions occupied by each genus; Flessa and Thomas 1985) for the family Apor-

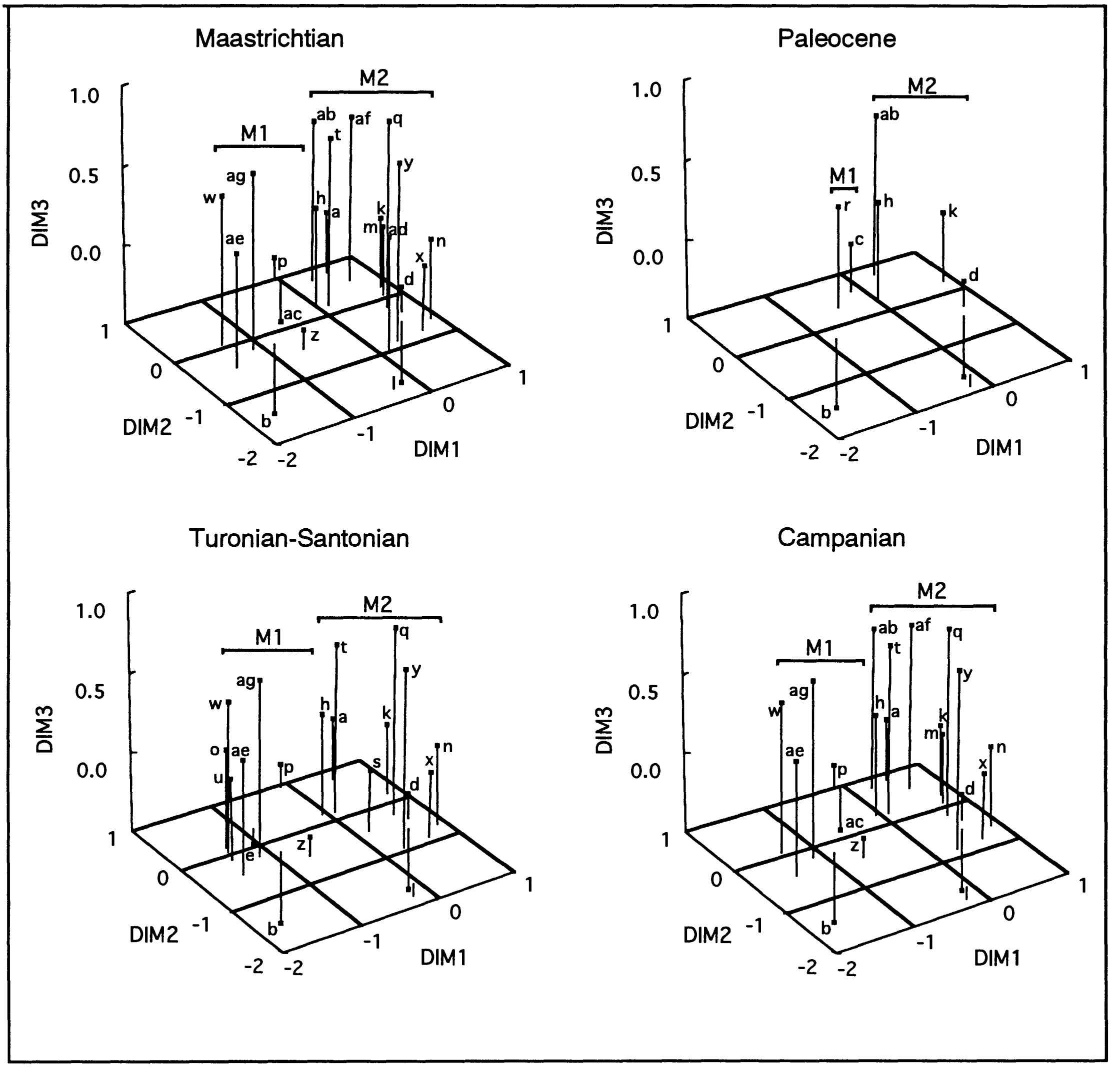

FIGURE 7. Temporal pattern of morphospace occupation of aporrhaid genera during the Late Cretaceous and Paleocene. Abbreviations as in figure 4. Note that with the sole exception of *Teneposita* (ac), all other genera originating during this time belong to the morphologic group M2. Thus, by the latest Cretaceous, M2 have much higher taxonomic diversity compared to M1. However, following the end-Cretaceous extinction, the two new Paleocene genera were both characterized by multidigitate apertural margins (M1).

rhaidae are strongly concave (fig. 8), indicating that most aporrhaid genera had narrow distributions, as seen in most other groups of organisms (see e.g., Anderson 1977; Hansen 1988). This pattern of geographic distribution was achieved by the Middle Jurassic and persisted throughout the rest of the Mesozoic. However, the shape of the distribution changed markedly following the Maastrichtian extinction, with the Paleocene fauna containing roughly equal proportions of broad- and narrow-ranging genera (fig. 8). Of the six Cretaceous genera that survived the mass extinction, three were widespread (i.e., occupying four or more geographic divisions: *Drepanochilus*, Maastrichtian [Maa] = 11, Paleocene [Pal] = 9; *Arrhoges*, Maa = 7, Pal = 6; *Aporrhais*, Maa = 4, Pal = 4), whereas two were narrow ranging (i.e., occupying three or fewer geographic divisions: *Dicroloma*, Maa = 1, Pal = 2; *Struthiochenopus*, Maa = 1, Pal = 1). No geographic data were available for the

TABLE 4. Temporal patterns of taxonomic and morphologic diversity (T.D. and M.D., respectively) of aporrhaid genera. Morphologic diversity calculated as the geometric mean of the range of the ordination scores (see text). M1 and M2 refer to the two morphologic groups defined by the ordination results. [Baj, Bajocian; Bth, Bathonian; Kim, Kimmeridgian; Tth, Tithonian; Vlg, Valanginian; Hau, Hauterivian; Brm, Barremian; Apt, Aptian; Alb, Albian; Cen, Cenomanian; Tur, Turonian; San, Santonian; Cmp, Campanian; Maa, Maastrichtian; Pal, Paleocene.]

	All genera		M1 genera		M2 genera	
Age	T.D.	M.D.	T.D.	M.D.	T.D.	M.D.
Pal	8	1.46	3	0.84	5	1.15
Maa	21	1.96	7	1.46	14	1.37
Cmp	20	1.91	7	1.47	13	1.33
Tur-San	20	1.91	9	1.44	11	1.33
Cen	18	1.83	9	1.43	9	1.15
Alb	15	1.61	7	1.32	8	1.06
Apt	15	1.59	6	1.16	9	1.06
Brm	12	1.35	5	0.82	7	0.94
Tth-Vlg	10	1.36	4	0.76	6	0.95
Bth-Kim	11	1.44	4	0.76	7	0.95
Baj	4	0.83	1	—	3	0.53

sixth genus (*Goniocheila*) during the Paleocene. Both *Dicroloma* and *Struthiochenopus* have a very poor fossil record during this time, and it is unclear if this is the cause or the effect of the narrow ranges. Of the victims of the Maastrichtian extinction, 13 genera were restricted whereas three were widespread. Of the three new Paleocene genera, *Araeodactylus* occupied four geographic divisions whereas *Maussenetia* and *Kangilioptera* occupied three and one divisions respectively. Although the pattern of survivorship is in the same direction as previously reported (Bretsky 1973; Fortey 1983; Jablonski 1986, 1989; Westrop & Ludvigsen 1987), the difference between widespread and restricted genera is not statistically significant (*G*-test, $0.1 > p > 0.05$). However, given the small number of genera involved in the present study, the power of statistical tests is suspect and hence the survivorship pattern documented should be interpreted with caution.

Biogeographic frequency distributions for the morphologic groups M1 and M2 from the Albian to Maastrichtian (when sampling is best) show that, in general, geographically restricted genera (i.e., occupying three or fewer geographic divisions) tend to predominate in both groups except during Turonian-Santonian when the M2 genera showed a more equitable distribution and during the Maastrichtian when the M1 genera showed a more equitable distribution (fig. 9). The reasons for these two anomalies are not clear, but sampling bias or mere statistical fluctuation cannot be ruled out (especially given the small number of M1 genera during the Maastrichtian). The major difference in the geographic distribution patterns of the two morphologic groups appears to be that M2, in addition to a number of very restricted genera, also contained a few widespread ones, a pattern absent from M1. As a result, M2 as a group was much more widespread geographically during post-Aptian times compared to M1 (fig. 10). This difference could very well be the expectation given the large difference in taxonomic diversity between the two groups. However, as discussed below, there is some empirical evidence to suggest that once attained, such widespread distributions helped to increase further the diversity of the morphologic group M2.

Discussion of Patterns of Diversification

As pointed out earlier, the evolutionary dynamics of aporrhaid gastropods should provide some insight into the nature of the biotic reorganization termed the Mesozoic Marine Revolution. In general, the Mesozoic history of the aporrhaids is characterized by two periods of taxonomic radiation, separated by some 50 m.y. of relative stability. This pattern is consistent with Vermeij's (1987) suggestion that changes during the Mesozoic may have proceeded in several more-or-less discrete steps separated by periods of relative stability.

While they both produced a substantial increase in global taxonomic diversity, the two radiations for aporrhaids had very different morphologic consequences. The initial radiation established two well-defined morphologic groups based on the nature of apertural modifications. These morphologic groupings persisted for the rest of the Mesozoic and provided the framework for later morphologic evolution of the aporrhaids. The second phase of radiation, beginning in the Cenomanian, primarily involved the M2 morphologic

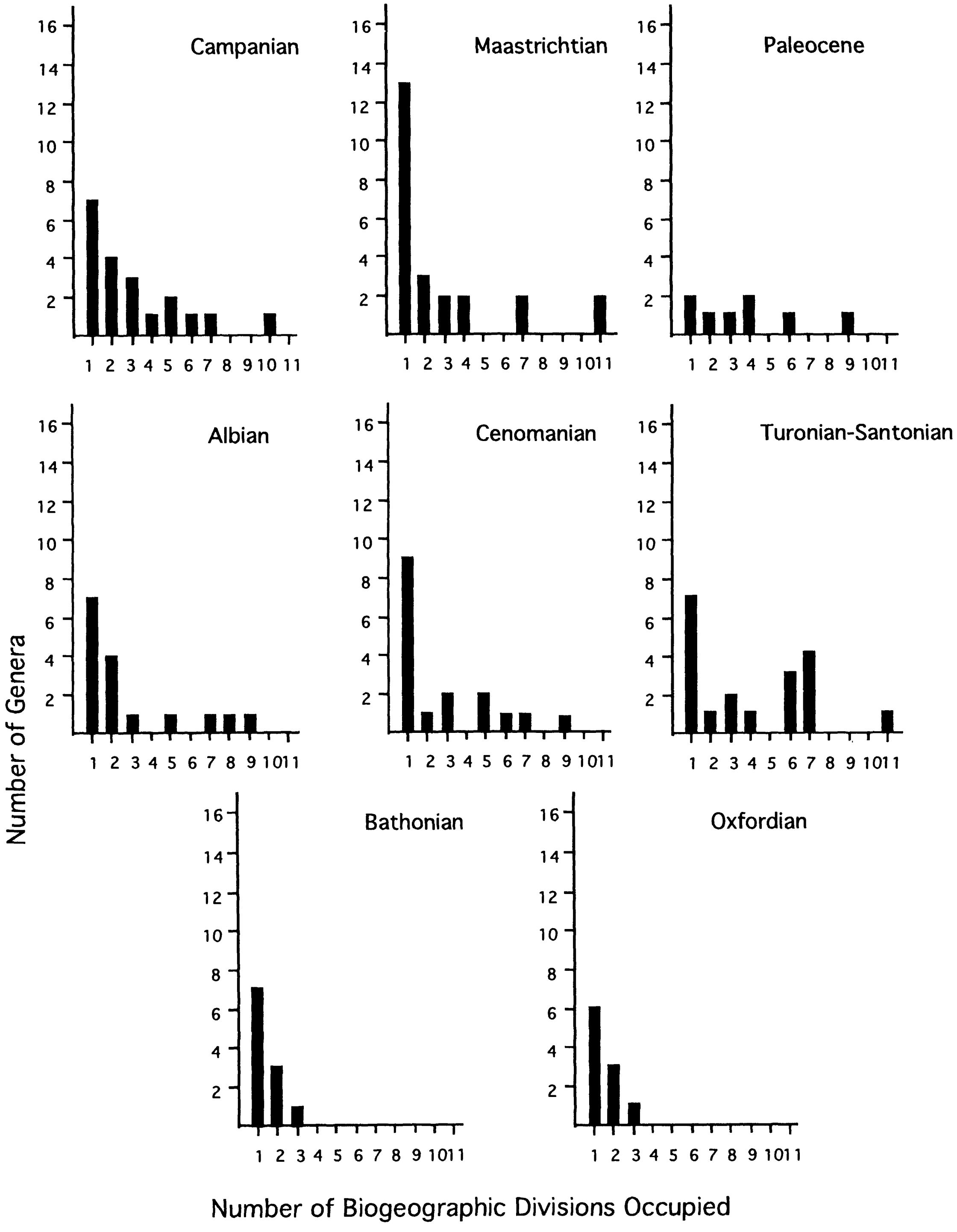

FIGURE 8. Biogeographic frequency distributions of aporrhaid genera from mid-Jurassic to Paleocene. Geographically restricted genera tend to predominate throughout the Jurassic and Cretaceous. However, during the Paleocene, following the end-Cretaceous extinction, a much more equitable distribution is apparent. Whether this equitable distribution is real or merely reflects the paucity of Paleocene marine sediments is not clear.

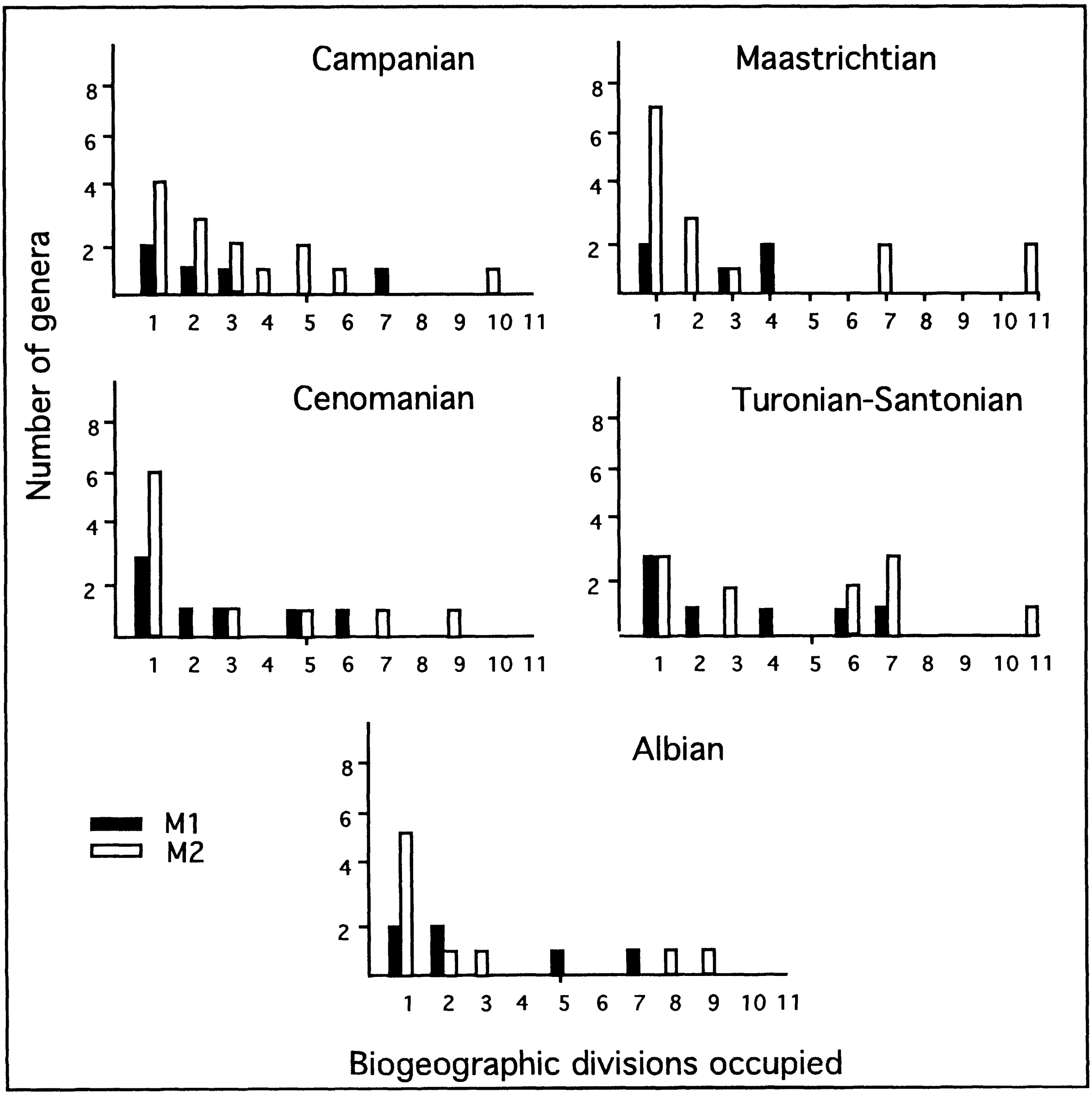

FIGURE 9. A comparison of the biogeographic frequency distributions of the two morphologic groups (M1 and M2) from the Albian to the Maastrichtian. The majority of genera in both groups had restricted geographic range. However, one major difference between the two groups is that M2 also contained a few widespread genera that were absent in M1.

group. The resulting difference in taxonomic diversity between the two groups was due not to higher extinction rates in M1 but largely due to differential addition of new taxa to M2: despite substantial increases in aporrhaid diversity between the Cenomanian and Maastrichtian, only one new M1 genus originated. This conclusion is also supported by the fact that there is no significant difference in the stratigraphic durations of the Jurassic and Cretaceous genera in the two groups (Kolmogorov-Smirnov test, $n = 29, p = 0.58$). If anything, M1 has lower extinction rates compared to M2, as shown by median stratigraphic durations (M1 = 64.7 m.y., M2 = 32 m.y.).

The increase in global diversity and changes in morphospace occupation described above were not accompanied by parallel increases in standing diversity of aporrhaid genera

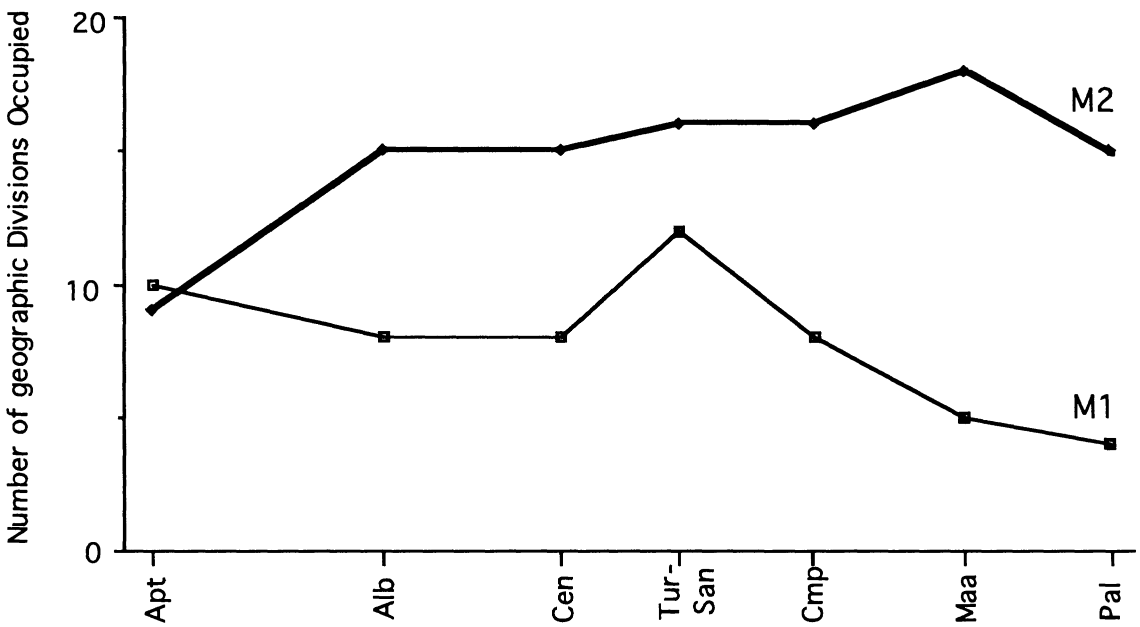

FIGURE 10. Biogeographic diversity (total number of biogeographic divisions occupied) of the morphologic groups M1 and M2 from Aptian to Paleocene. As a group M2 is much more widespread during this time interval than M1.

within all geographic areas. While standing diversity within some areas increased in concert with the global radiation, it either decreased or remained constant in other areas. This produced remarkably constant average taxonomic diversities within and between geographic areas over nearly 50 m.y. Thus, for the aporrhaid gastropods, the consequences of the Cretaceous reorganization appears to have been manifested differently at different geographic/ecological scales, a phenomenon that has been noted in other studies of taxonomic radiation (see Lidgard et al. [1993] for bryozoans, and Sepkoski [1988] for Paleozoic marine invertebrates).

The Albian radiation changed the biogeographic structure of the aporrhaids by giving rise not only to a number of geographically restricted genera but also to a few very widespread ones. This change, however, was not distributed evenly between the two morphologic groups: the biogeographic diversity of the M1 group decreased from the Aptian-Albian to Maastrichtian while that of M2 increased substantially (fig. 10). The taxonomic, morphologic, and biogeographic data presented in this study all reveal the same pattern, i.e., differential success of aporrhaids with relatively simple apertural margins during the Late Cretaceous. This pattern contrasts strongly with that documented for Cretaceous *Montastraea*-like corals, where there were no origination biases with respect to morphology despite a number of radiations (Budd and Coates 1992). This "nonprogressive evolution" in corals was attributed to the constraints of corallite size and the number of septa (Budd and Coates 1992). Unfortunately, no such singular cause can be identified for the differential evolutionary success of the simpler aporrhaid morphotypes.

Hypotheses of Processes (with Some Caveats)

Directional trends in patterns of morphospace occupation at higher taxonomic levels can result from a variety of processes including species selection, species sorting, asymmetrical changes in variance due to the presence of an absorbing or reflecting boundary, and directional speciation resulting from phylogenetic and/or developmental constraints (e.g., Lauder 1981; Vrba 1984, 1989; Vrba and Gould 1986; Gould 1988, 1990; Budd

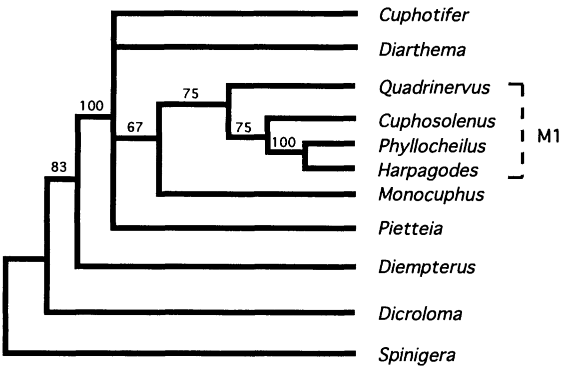

FIGURE 11. Phylogenetic relationships among genera of aporrhaids that originated during the mid-Jurassic radiation. The phylogeny is based on a matrix of 23 morphologic characters, of which 21 were binary and 2 unordered multistate. The analysis was done in PAUP, ver. 3.0q (Swofford 1991) using the simple addition and TBR branch-swapping options under the "heuristic" search settings. Since the ancestry of the Aporrhaidae is not known, the oldest genus of the ingroup (*Spinigera*) was specified as a working outgroup. PAUP produced 12 shortest trees (length = 42). The tree illustrated here represents the 50% majority-rule consensus of the 12 trees. Rohlf's consensus index for the consensus tree is 0.756. A comparison of the branching order in the cladogram with the order of stratigraphic occurrence indicates one major discrepancy: the genus *Phyllocheilus,* which occupies the most derived position on the tree, is stratigraphically older than all other taxa except *Spinigera, Pietteia,* and *Dicroloma.* Given the poor quality of the marine fossil record during the Bajocian, it is quite likely that this discrepancy is due to taphonomic factors. The phylogenetic relationships indicate that the morphologic group M1 was monophyletic during the Jurassic.

and Coates 1992). These mechanisms, of course, are not mutually exclusive and trends can often result from one or more of these factors acting in concert. The following discussion attempts to highlight some of the potential processes underlying the macroevolutionary patterns documented here.

The Phylogenetic Aspect.—Hypotheses about macroevolutionary processes can be rigorously tested only within a historical framework, one that is reflected in a well-resolved phylogeny. In fact, Lauder (1981) has argued that a phylogenetic hypothesis serves as a null hypothesis of temporal changes in morphology and only significant deviations from this pattern require other explanations. As is the case with most groups of marine organisms, the phylogeny of aporrhaid gastropods is still poorly known. A preliminary cladistic analysis of the relationships among genera of aporrhaids that originated during the Jurassic was undertaken using 23 morphologic characters. While the characters used in the cladistic analysis were similar to those used to define the aporrhaid morphospace, there is no reason to assume that the two analyses will produce similar results. The distribution of taxa in morphospace reflects overall phenetic similarity of both apomorphic and plesiomorphic characters while the cladistic topology presumably reflects the "routes of colonization" of that particular morphospace by apomorphic characters (Fisher 1986, 1991).

The results of the phylogenetic analysis indicate that prior to the Cretaceous radiation, the morphologic group M1 was a monophyletic clade derived from an early member of M2 (*Monocuphus*) (fig. 11). Thus, at least during the early phase of the evolutionary history of aporrhaids, there was a strong phylogenetic component to the morphologic grouping suggesting that the initial radiation of the M1 genera could simply reflect a phylogenetic link with higher origination rates (sensu Gould 1982). The phylogeny of the Cretaceous aporrhaid genera is not yet resolved: homoplasy is much more pervasive, and the ratio of characters to taxa is less favorable. The only available phylogeny of some of the Cretaceous aporrhaids is that of Korotkov (1993), which is based solely on stratophenetic evidence and includes only about half the genera used here. Korotkov's scheme indicates that during the Jurassic and Cretaceous M1 genera formed a monophyletic clade (except *Helicaulax* which falls with the M2 genera), while M2 genera were divided into two clades. Thus, morphologic patterns of evolution seem to closely parallel phylogenetic patterns. However, Korotkov's phylogeny is based on a qualitative notion of relationships and hence is at best considered a preliminary hypothesis (which needs to be tested through rigorous phylogenetic analysis using shared derived characters) rather than a definitive answer. Therefore, it remains to be seen whether the morphologic origination bias during the Cretaceous radiation was partly due to a fortuitous phylogenetic link with increased origination rates (sensu Gould 1982) as suggested by Korotkov's (1993) phylogeny, or whether the pattern cut across phylogenetic lines, thereby indicating a larger role of selective forces, either biotic or abiotic.

The Role of Predation Pressure.—Vermeij (1987) identified a number of potential biotic and abiotic causes for the late Mesozoic reorganization. These include escalation between predators and prey, climatic and tectonic change, formation of geographic barriers, and changes in primary productivity (Vermeij 1987). It is possible that some or all of these played a role in generating the patterns described in this paper. Unfortunately, the available data do not permit rigorous testing of these hypotheses. However, as discussed below, there is some evidence to suggest that predator-prey interactions could have played a role in generating the aporrhaid evolutionary trends.

One of the main components of Late Cretaceous escalation was the rise and diversification of durophagous predators and predatory gastropods (Vermeij 1987). This increase in predation pressure correlates well with both increased antipredatory sculpture in various groups of mollusks and increased incidence of repaired shell damage (Vermeij 1977, 1987). In many groups of gastropods, reinforced apertural margins resist peeling and crushing by decapod crustaceans, so that species under high predation pressure tend to have narrow and reinforced apertures (Zipser and Vermeij 1978; see also Vermeij 1987). Perron (1978a) observed that the adults of the Recent aporrhaid *Arrhoges occidentalis* with fully developed apertural margins appear to be less vulnerable to predation by the crab *Cancer irroratus* than conspecific juveniles lacking the apertural modification. Merz (1979) experimentally demonstrated that the apertural modifications in *Strombus alatus* also serve an antipredatory function (also see Savazzi 1991). In both of these cases, the apertural modifications would be categorized as morphologic group M2. Because the morphologic change in the aporrhaids also coincides well with the inferred rise in predation pressure, the differential success of the M2 genera might be attributable to escalation between predators and prey. This implies that the apertural modifications of the M2 genera were more resistant to predation than those of M1 genera. However, the functional significance of the various types of apertural modifications is unclear at present, and hence the above hypothesis is hard to evaluate. Qualitative observations on the morphology of the apertural modifications of Cretaceous aporrhaids suggest a possible difference in strength between the two types of apertures as multidigitate apertures, in a number of cases, were remarkably thin compared to the simpler ones. In fact, in some multidigitate genera (e.g., *Pterocerella*) the apertural digits were connected only by a paper-thin layer of shell material. There are, however, exceptions to this generalization and an obvious case would be the comparison between the two Recent species *Aporrhais pespelecani* and *Arrhoges occidentalis.* The apertural margins in both of these species appear to be equally sturdy although *Aporrhais pespelecani* is characterized by multidigitate apertures while *Arrhoges occidentalis* has M2 type of aperture. It is, however, possible that the thickening of the apertural margin of the genus *Aporrhais* is a Cenozoic phenomenon as the apertures of the few available Cretaceous specimens of this genus appeared to have been much weaker.

I attempted a preliminary empirical test of the antipredatory hypothesis by searching for repaired shell damage in various species of Mesozoic aporrhaids. In the several hundred Jurassic and Cretaceous specimens examined, incidences of repaired shell damage proved to be rare and no difference between the two morphologic groups was apparent. However, in at least one well-preserved Late Cretaceous assemblage (Ripley Formation), high incidences of repaired sublethal damage have been documented for *Graciliala calcaris,* a species that would be categorized as M2 in this study (Vermeij and Dudley 1982). It should also be pointed out that, as with repaired shell damage, incidences of drilling predation are low overall among the Mesozoic aporrhaids. Interestingly, the highest incidence of drilling predation on aporrhaids is in the Albian Blackdown Greensand of England (Taylor et al. 1983), and not in the Late Cretaceous. Because the empirical data on predation are inconclusive, one way to resolve this question would be to evaluate experimentally the handling costs associated with various aporrhaid morphologies and test for differences between the two major morphologic groups. As LaBarbera (1981) has shown, this is possible even for extinct species. If the morphologic type M2 is indeed more resistant to predation than M1, then that, combined with the fact that the success of M2 is due to an origination bias, would support the contention that while predator–prey interactions are not important agents of extinction they can mediate differential originations. Selection due to predation must then be considered as an important macroevolutionary process (Vermeij 1987).

The Effects of Geographic Range.—The biogeographic frequency distributions of both morphologic groups of the aporrhaids resemble the classic hollow curve (see Anderson 1977; Flessa and Thomas 1985). They differ in post-Albian times, however, in that the morphologically simple genera (M2) tend to be more widespread compared to the multidigitate group (M1) (fig. 10). As noted earlier this could simply be due to the higher taxonomic diversity of M2. Even so, such widespread distribution, once attained, could still contribute to the subsequent increase in the diversity of the group (Rosenzweig 1975, 1992). In Cretaceous *Montastraea*-like corals, speciation was apparently associated with widespread groups and the descendant taxa were more narrowly distributed (Budd and Coates 1992). As ancestor–descendant relationships are poorly known for most Cretaceous aporrhaids, the relationship between origination and geographic range cannot be evaluated for all taxa. However, in the cases where the ancestor–descendant relationships are clear, it is evident that the Cretaceous aporrhaids exhibit a pattern similar to the *Montastraea*-like corals in that origination tends to be associated with widespread taxa. For example, Sohl (1960) showed that the widespread genus *Drepanochilus* (occupying ten biogeographic divisions during the Campanian) is clearly ancestral to *Graciliala* (occupying two biogeographic divisions during the same time). Popenoe (1983) suggested that the three genera *Gymnarus, Pyktes,* and *Tephlon* are closely related. The oldest of the three, *Gymnarus* was widespread (occupying seven divisions during the Turonian–Santonian), while *Pyktes* and *Tephlon* each occupied only one biogeographic division during the Turonian–Santonian and Maastrichtian, respectively. These results from two very different groups of organisms (*Montastraea*-like corals and aporrhaid gastropods) suggest a more important role for geographic range during the Cretaceous radiations than previously recognized.

Conclusions

1. The Mesozoic history of the family Aporrhaidae is characterized by two major radiations, separated by a period of overall stability. While both radiations increased the taxonomic diversity of the family, they had very different morphologic consequences.

2. The initial radiation during Bajocian–Bathonian times established two large morphologic groups within the aporrhaids, based mainly on differences in the shape of the apertural margins. The post-Albian radiation of the family saw higher origination rates and hence increased generic diversity of the morphologic group with simpler apertural margins. At the same time genera with elaborate multidigitate apertural margins declined in importance.

3. A preliminary phylogenetic analysis suggests that prior to the Cretaceous radiation the aporrhaid genera characterized by multidigitate apertures formed a monophyletic group. Thus, during the early phase of the evolutionary history of aporrhaids there was a strong phylogenetic component to the morphologic grouping suggesting that the initial radiation of the multidigitate group could reflect a phylogenetic link with higher speciation rates. Whether this pattern is also true for the second radiation remains to be seen, as the phylogeny of the Cretaceous aporrhaid genera is not yet resolved.

4. The causal factors behind the success of aporrhaid genera characterized by simpler apertural margins is still unclear. However, there is some evidence to suggest that predator–prey interactions and geographic range of genera could have played important roles.

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Appendix 1

The following genera (discrete species groups) of aporrhaids have been recognized in this study. Each of these genera represents a distinct type of apertural morphology. Note that *Struthioptera* Finlay and Marwick and *Austroaporrhais* Zinsmeister have not been treated as separate genera here. The former is probably a subgenus of *Arrhoges* while the latter probably belongs with *Dicroloma.*

Genus	Type species
Anchura Conrad 1860	*Anchura abrupta* Conrad
Aporrhais DaCosta 1778	*Aporrhais quadrifidus* DaCosta = *A. pespelecani* (Linné)
Araeodactylus Harris and Burrows 1891	*Ischnodactylus plateaui* Cossmann
Arrhoges Gabb 1868	*Chenopus occidentale* Beck
Cuphosolenus Piette 1876	*Pterocera tetracer* d'Orbigny
Cuphotifer Piette 1876	*Rostellaria hamulus* Deslongchamps
Diarthema Piette 1864	*Pterocera paradoxa* Deslongchamps
Dicroloma Gabb 1868	*Pterocera lorierei* d'Orbigny
Diempterus Piette 1876	*Diempterus lonqueueana* Piette
"*Dimorphosoma*" Gardner 1875	Gardner designated *Aporrhais calcarata* Sowerby as the type of this genus but *A. calcarata* belongs in *Drepanochilus.* However, other specimens assigned here do constitute a distinct taxon and hence "*Dimorphosoma*" needs to be revised.
Drepanochilus Meek 1864	*Rostellaria americana* Evans and Shumard
Goniocheila Gabb 1868	*Drepanochilus* (*Goniocheila*) *liratum* (Conrad) Cossmann
Graciliala Sohl 1960	*Anchura* (*Drepanochilus*) *calcaris* Wade
Gymnarus Gabb 1868	*Pugnellus* (*Gymnarus*) *manubriatus* Gabb
Harpagodes Gill 1870	*Strombus pelagi* Brongniart
Helicaulax Gabb 1868	*Rostellaria ornata* d'Orbigny
Lispodesthes White 1875	*Anchura nupitalis* White
Maussenetia Cossmann 1904	*Maussenetia staadti* Cossmann
Monocuphus Piette 1876	*Pterocera camelus* Piette
Perissoptera Tate 1865	*Rostellaria reussi* Tate
Phyllocheilus Gabb 1868	*Strombus ponti* Brongniart
Pietteia Cossmann 1904	*Rostellaria hamus* Deslongchamps
Pterocerella Meek 1864	*Harpago tippana* Conrad
Pugnellus Conrad 1860	*Pugnellus densatus* Conrad
Pyktes Popenoe 1983	*Pyktes aspris* Popenoe
Quadrinervus Cossmann 1904	*Pterocera ornatus* Buvignier
Spinigera d'Orbigny 1850	*Ranella longispina* Deslongchamps
Struthiochenopus Zinsmeister	*Perissoptera nordenskjoldi* Steinmann and Wilckens
Teneposita Loch 1989	*Teneposita laeva* Loch
Tephlon Popenoe 1983	*Pugnellus tumidus* Gabb
Tessarolax Gabb 1864	*Tessarolax distortus* Gabb
Tibiaporrhais Elder 1990	*Nudivagus? cooperensis* Stephenson
"*Tridactylus*" Gardner 1875	*Aporrhais cingulata* Pictet and Roux
Specimens of the following taxa were not available for examination and hence the assignments are only tentative	
New genus 1	*Aporrhais luganicus* Blank 1972 probably belongs to a new genus.
New genus 2	*Helicaulax pozaryskii* Abdel-Gawad could represent a new genus.
Kangilioptera Rosenkrantz 1970	*Anchura* (*Kangilioptera*) *ravni* Rosenkrantz
Kaunhowenia Abdel-Gawad	*Aporrhais* (*Helicaulax*) *carinifera* Kaunhowen 1897. This was assigned to a new genus *Kaunhowenia* by Abdel-Gawad which is probably valid.

Appendix 2

Taxonomic differentiation between pairs of geographic divisions expressed using the Jaccard coefficient. The calculations only include geographic divisions with non-zero values. Divisions with gaps excluded from this analysis as it is not clear whether the absences are real or taphonomic artifacts. (CP, Coastal Plain; NA, N. Africa; NE, N. Europe; SE, S. Europe; CE, C. Europe; WI, Western Interior; Ant., Antarctica; Aust., Australia; Pac., California, Washington, Oregon.)

Area pair	Paleocene	Campanian-Maastrichtian	Cenomanian-Santonian	Aptian-Albian
CP-NA	0.33	0.2	0.4	0.37
CP-NE	0.17	0.32	0.33	0.33
CP-SE	0	0.15	0.18	0.25
CP-CE	0.25	0.08	0.3	0.33
CP-Crimea	0.4	0.23	0.33	0.5
CP-WI	0.33	0.27	0.37	0.17
CP-Ant.	0	0	0	0
CP-Aust.	0.5	0.31	0.12	0.17
CP-Japan	0.33	0.23	0.71	0.43
CP-Pac.	0.25	0.31	0.33	0.29
NA-NE	0	0.31	0.43	0.27
NA-SE	0	0.17	0.62	0.27
NA-CE	0.5	0.2	0.3	0.17
NA-Crimea	0.25	0.33	0.5	0.33
NA-WI	1	0.57	0.22	0.2
NA-Ant.	0	0	0	0
NA-Aust.	0.33	0.29	0.12	0.2
NA-Japan	1	0.33	0.33	0.29
NA-Pac.	0.5	0.18	0.2	0.14
NE-SE	0.25	0.17	0.36	0.35
NE-CE	0.2	0.08	0.27	0.14
NE-Crimea	0.6	0.25	0.38	0.21
NE-WI	0	0.29	0.13	0.07
NE-Ant.	0	0	0	0.06
NE-Aust.	0.17	0.23	0.15	0.07
NE-Japan	0	0.15	0.29	0.29
NE-Pac.	0.2	0.18	0.2	0.21
SE-CE	0	0.5	0.33	0.22
SE-Crimea	0	0.67	0.37	0.2
SE-WI	0	0.14	0.11	0.11
SE-Ant.	0	0	0	0.09
SE-Aust.	0	0.5	0.33	0.11
SE-Japan	0	0.25	0.22	0.18
SE-Pac.	0	0.11	0.1	0.2
CE-Crimea	0.5	0.33	0.22	0.25
CE-WI	0.5	0.17	0.25	0.5
CE-Ant.	0	0	0	0
CE-Aust.	0.25	0.25	0.14	0.5
CE-Japan	0.5	0.33	0.22	0.5
CE-Pac.	1	0.12	0	0.25
Crimea-WI	0.25	0.29	0.29	0
Crimea-Ant.	0	0	0	0
Crimea-Aust.	0.4	0.4	0.4	0
Crimea-Japan	0.25	0.5	0.25	0.4
Crimea-Pac.	0.5	0.22	0.43	0.5
WI-Ant.	0	0	0	0
WI-Aust.	0.33	0.25	0.2	1
WI-Japan	1	0.5	0.29	0.25
WI-Pac.	0.5	0.56	0.12	0
Ant.-Aust.	0	0	0	0
Ant.-Japan	0	0	0	0
Ant.-Pac.	0	0	0	0.2
Aust.-Japan	0.33	0.17	0.17	0.25
Aust.-Pac.	0.25	0.2	0.17	0
Japan-Pac.	0.5	0.37	0.25	0.4
Means	0.27 ± 0.04	0.23 ± 0.02	0.23 ± 0.02	0.22 ± 0.02