Triassic bivalves and the initial marine Mesozoic revolution: A role for predators?

Christopher A. McRoberts*

Department of Geology, State University of New York, Cortland, New York 13045, USA

ABSTRACT

Marine bivalves document the long-term increase in generic richness through the early Mesozoic. Following the end-Permian crisis, the Early Triassic was marked by a gradual recovery in generic richness (57 Induan and 66 Olenekian genera). Diversity slowly increased in the Middle Triassic (98 Anisian and 121 Ladinian genera) and peaked in the Late Triassic (171 Carnian, 165 Norian, and 143 Rhaetian genera). These data support earlier hypotheses that the recovery following the end-Permian extinction was very gradual and was not completed (in terms of both richness and ecologic complexity) until the Ladinian. Although a Carnian-Norian extinction is not evident in the data and may be a regional event limited to the Tethyan realm, the end-Triassic extinction is profound—fewer than 30 genera (<35%) survived into the Jurassic. Diversity metrics are not equally distributed among bivalve living habits. The generally epifaunal Pteriomorphia and Isofilibranchia exhibit higher extinction rates compared to the ordinarily infaunal Heteroconchia (especially the Veneroida and Trigonoida). This pattern of selective extinction led to a gradual increase in generic richness of infaunal suspension feeders through most of the Triassic. Contrary to previous hypotheses, this increase in infaunalization may not have been related to the evolutionary expansion of major predatory groups (e.g., shell-crushing cephalopods, crustaceans, sharks, fish, and reptiles), which had typically low abundances and limited distribution during the Triassic. Drilling predators, although present during the Triassic, are not considered to be prominent causes of mortality among bivalves. Instead, the infaunalization of bivalves during the Triassic may have been due to several interconnected abiotic and biotic causes associated with the recovery after the end-Permian mass extinction.

Keywords: Triassic, Bivalvia, diversity, adaptive radiation, paleoecology.

INTRODUCTION

Biotic radiations—evolutionary bursts involving increasing taxonomic diversity and evolutionary innovation—typically follow mass extinctions and are characterized not only by the recovery of surviving taxa, but also by a marked proliferation of new plant and animal groups. One of the most spectacular radiations of the Phanerozoic is the marine Mesozoic revolution (MMR) that records the diversification of plant and animal taxa following the end-Permian mass extinction (Vermeij, 1977). The MMR marks the establishment of a marine fauna with an essentially modern aspect characterized by bivalve and gastropod mollusks, bony fishes, gymnolaemate bryozoans, echinoids, and certain crustaceans, representing an increase in trophic variety ranging from deep infaunal suspension feeders to active nektonic carnivores (Sepkoski, 1981).

One hypothesis explaining the MMR is that adaptations and behaviors within certain invertebrate groups, such as bivalve and gastropod mollusks, may in part have been driven by escalating predator-prey interactions (Vermeij, 1987). This argument contends that many characteristics in these mollusks were a result of competitive selective pressures imposed by predatory organisms. Preexisting or newly evolved adaptations in bivalves to counter these predatory pressures include a wide variety of traits such as escape behaviors, thicker shells, and, perhaps most important, characteristics enabling bivalves to colonize infaunal habitats out of the reach of surface-dwelling predators (Stanley, 1968, 1977). Infaunalization is demonstrated by the fact that Paleozoic and early Mesozoic bivalve faunas have a much greater proportion of epifaunal taxa than do modern bivalve faunas.

A shortcoming of the escalation explanation of the MMR is that while the MMR originated in the Triassic following the end-Permian crisis, dominant groups to which predatory behavior can be attributed did not evolve or were not very abundant until the Cretaceous or Paleogene. One explanation for this apparent contradiction may lie in the real possibility that most Triassic predators did not leave clear evidence of predation or that such evidence is masked by taphonomic agents of destruction. Alternatively, this apparent inconsistency questions the assertion that the MMR was indeed driven by predatory pressures and instead suggests that many so-called predatory adaptations were in fact preadaptions and unrelated to coevolving predatory groups. One way to approach this problem is to better document the pattern of diversification among prey groups. This paper documents diversity changes in living strategies of bivalve mollusks, one of the key faunal components in the MMR and the establishment of the modern fauna.

DATA

I compiled generic and subgeneric data from primary and summary literature sources including a compendium of bivalve genera (J. Sepkoski, 1996, personal commun.), supplemented by museum and field collections. These data were checked and amended for possible synonymy and stratigraphic occurrences. I based the range of each genus upon the cumulative and interpolated time between first and last occurrences. I calculated originations as first occurrences and extinctions as last occurrences. Diversity is recorded as generic richness and
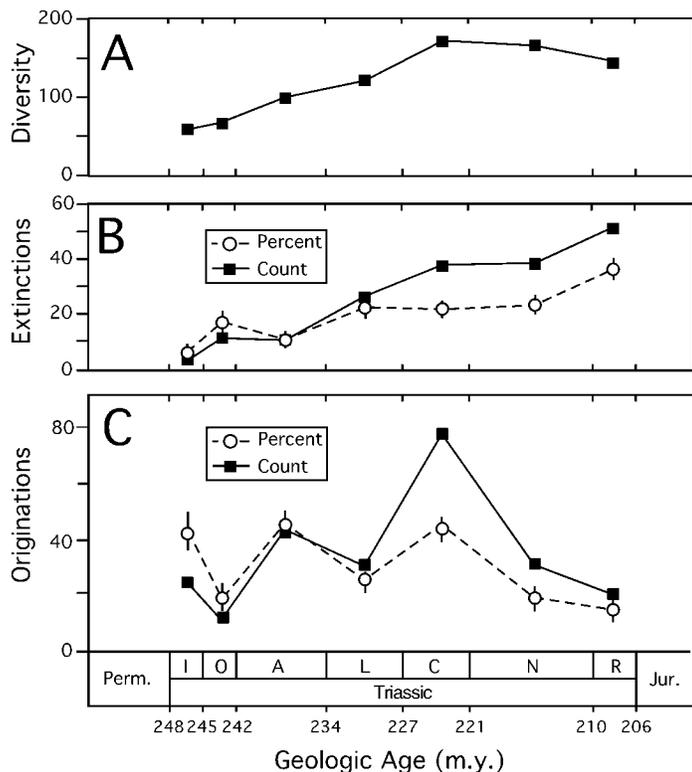
*E-mail: mcroberts@cortland.edu.

Figure 1. Triassic diversity, extinction, and origination plots. A shows generic richness. In B and C, extinctions and originations are shown as number and percentage of infaunal and epifaunal genera through the Triassic. Bars on percentages (circles) represent one standard error. Perm.— Permian; Jur.— Jurassic. Stages: I—Induan, O—Olenekian, A—Anisian, L—Ladinian, C—Carnian, N—Norian, R—Rhaetian. Time scale is from Gradstein et al. (1995).
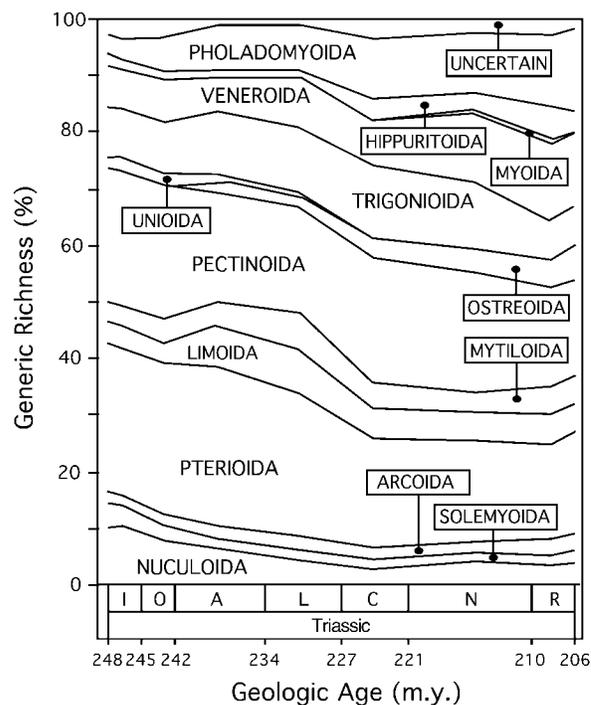

Figure 2. Triassic bivalve richness showing proportion of genera within bivalve orders. Note relative increase of generally infaunal orders Pholadomyoida and Veneroida at expense of generally epifaunal orders Pterioida and Pectinoida. Stage abbreviations as in Figure 1.

is simply the number of bivalve genera occurring (or interpolated) during a particular stage, irrespective of abundance. I assigned each genus a living habit that incorporates the animals' relationship to the substrate, mobility, and feeding habit.

The data are recorded at the stratigraphic resolution of stage, even though Triassic stage boundaries do not yet have defined stratotypes. To avoid some of the more contentious issues surrounding Triassic stage boundaries, the scale used herein is that of Gradstein et al. (1995), which includes the Parvis zone as the base of the Induan Stage, the Aon zone as the base of the Carnian Stage, and the Reticulatus zone as the base of the Rhaetian Stage.

These generic and range data may be subject to systematic, temporal, and preservational biases. Although underestimating the taxonomic diversity and ranges, such error can be assumed to be generally independent of living habit. An additional point of concern is that the data may contain polyphyletic or paraphyletic genera. Inclusion of paraphyletic and polyphyletic genera may lead to equivocal temporal diversity metrics (e.g., Patterson and Smith, 1987); however, such errors are considered to be of lesser importance at the generic level than at higher taxonomic rank (e.g., families) and may be further lessened if the genera are taken to be proxies of underlying species patterns (see Sepkoski, 1987).

PATTERNS OF DIVERSIFICATION

The Early through Middle Triassic was marked by a steady increase in generic diversity of bivalve genera (Fig. 1), from 57 in the Induan to 66 in the Olenekian. Diversity sharply increased in the Middle Triassic (98 Anisian and 121 Ladinian genera) and reached a peak in the early Late Triassic (171 Carnian genera) before gradually declining through the remainder of the Late Triassic (165 Norian and 143

Rhaetian genera). These diversity metrics are not distributed equally among bivalve orders (see Fig. 2). The most abundant orders include the Pterioida, Pectinoida, Trigonoida, Veneroida, and Pholaomyoida, which together contain 63%–78% of Triassic genera.

Extinction patterns of bivalve genera show a gradual increase in extinction intensity throughout the Triassic (Fig. 1B). Generic extinctions increased from just over 5% to nearly 40% for the end-Triassic event at the Rhaetian. It is likely that the end-Carnian extinction peak recognized by several workers (e.g., Benton, 1986; Johnson and Simms, 1989) is a regional artifact affecting mostly Tethyan faunas of Alpine and northwestern Europe (McRoberts, 1996). Conversely, the end-Triassic signature is quite robust, being clearly delimited in a variety of disparate taxa across the globe (e.g., Hallam, 1981; McRoberts and Newton, 1995; Olsen et al., 1988). When a subset of the data (excluding detritus feeders and aberrant forms, such as the megalodontiids and dicerocardiids, which probably employed photosymbionts) is examined, there are distinct differences in extinction rates between infaunal and epifaunal suspension feeders (Fig. 3A). Except during the Norian and Rhaetian Stages, epifaunal bivalves underwent, on average, nearly 10% greater extinction than infaunal genera. This difference is both statistically ($p < 0.01$) and ecologically significant.

Origination rate peaks in the Induan, Anisian, and especially the Carnian document greater than 44% new genera (Fig. 1C). The other stages generally show <25% new taxa. The peak in Carnian originations most probably reflects the diverse and well-studied assemblages of the Cassian fauna of northern Italy. In contrast to extinction rates, the similarity in origination rates between infaunal and epifaunal suspension feeders is insignificant (Fig. 3B).

Differential extinction rates between infaunal and epifaunal suspension-feeding bivalves have led to an increase in the percentage of infaunal bivalve taxa during the Triassic. This effect can be observed in the increase in relative proportions of genera within typically infaunal bivalve orders (e.g., Veneroida, Pholadomyoida, and Triginoida) while the number of genera within mostly epifaunal orders (e.g., Pter-
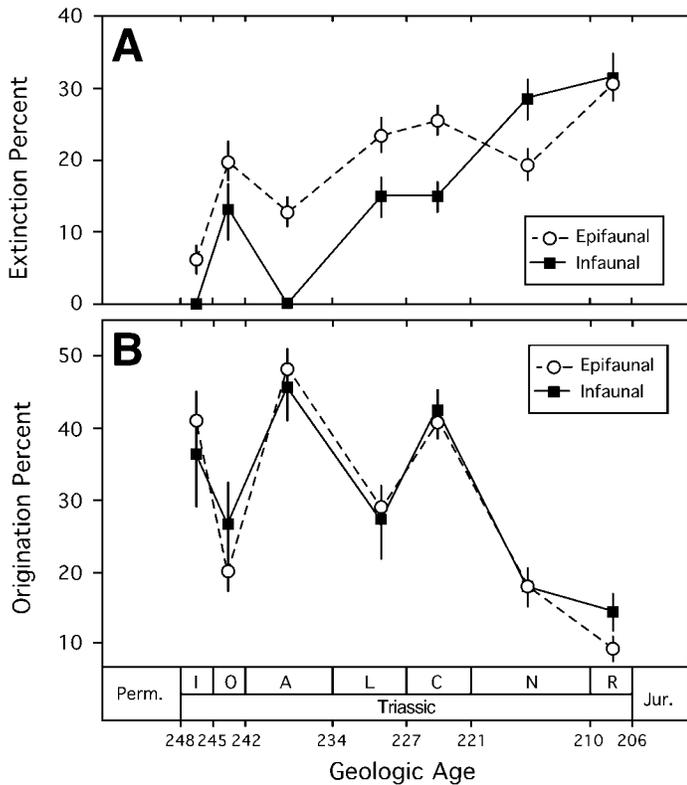
Figure 3. Origination and extinction rates of infaunal vs. epifaunal suspension-feeding bivalves. A: Percent extinction; shows clear differential extinction rates during Middle and Upper Triassic. B: Percent origination of infaunal and epifaunal bivalves showing no significant difference between infaunal and epifaunal origination rates. Bars represent one standard error. Time scale and stage abbreviations as in Figure 1.

ioida, and Pectinoida) remained constant or increased at a lesser rate (see Fig. 2). This trend of post-Paleozoic infaunalization has been previously recognized at different temporal scales within the Bivalvia (e.g., Stanley, 1968) and across other animal groups as well (e.g., Thayer, 1979).

ROLE FOR PREDATORS?

As described by Vermeij (1987), one of the driving forces in the MMR was the effect of predatory pressures and its subsequent effect on natural selection. Predation on bivalve mollusks can take several forms, such as breakage, forced entry, or shell drilling. Unfortunately, all but shell drilling are difficult to ascertain from fossils, because the effects of predatory crushing are similar to many taphonomic agents of destruction by normal current and wave action.

Potential molluscivores include several groups of shell-crushing fish (some teleost and chrondrichthians), ichthyosaurs, placodont reptiles, certain decapod crustaceans (brachyuran crabs and spiny lobsters), cephalopods with calcified jaws, and certain asterozoans (Fig. 4). Ichthyosaur remains are common in many marine Triassic deposits, and although many of the species more likely preyed on mid-water nekton, some of the taxa, especially during the Early and Middle Triassic, had heterodont dentition with blunt rear teeth capable of crushing bivalve shells (Massare and Callaway, 1990). Likewise, placodont reptiles were capable of preying on bivalves and may have had certain adaptations facilitating a molluscivore habit (Mazin and Pinna, 1993). However, because placodonts were not very abundant and are only known from the Middle and Upper Triassic of the Germanic basin and western Tethys, it is not likely that they could have affected the global diversity of bivalves. As yet unidentified predatory drilling snails may also have been present during the Triassic. Drilling predation seems to have been very rare through all of the Triassic and into even the Late Cretaceous (Kowalewski et al., 1998). Rare occurrences in bivalves of drill holes that may be predatory in origin have been noted from the Upper Triassic of northern Italy (Fürsich and Jablonski, 1984) and Oregon and Alaska (Newton, 1983). Citing evidence of Early Jurassic gastropod predatory boreholes from the United Kingdom, Harper et al.
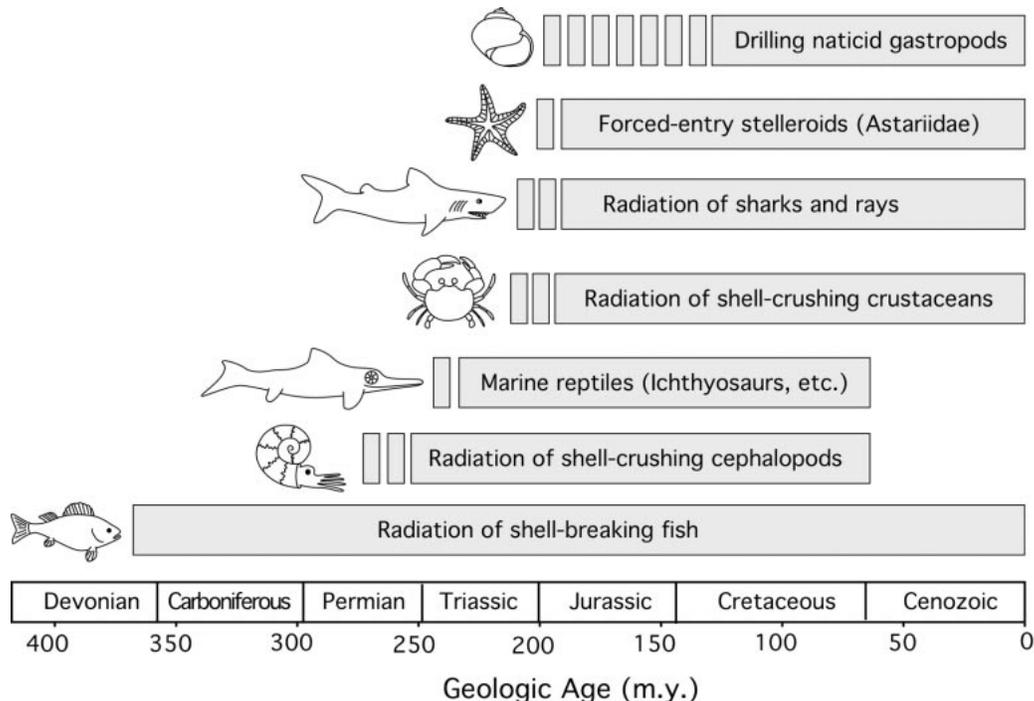

Figure 4. Representation of first appearances and diversification of major marine molluscivores. Adapted from Vermeij (1987) and Carter et al. (1998).

(1998) suggested that this lack of predatory record may be due to preservational bias. However, even exceptionally preserved Triassic bivalve faunas, such as occur in the Cassian (Carnian, Italy) and Kössen (Rhaetian, Austria) Formations, lack clear and convincing evidence of abundant mortality by drilling predators. These data suggest that whereas drilling predation may have been occurring, it was not a major factor in bivalve mortality during the Triassic. Although predation on bivalves was certainly occurring during the Triassic, most groups of common molluscivores had not yet evolved. With the possible exception of ammonoids, the molluscivores that were around during the Triassic were likely not sufficiently abundant to achieve the dramatic differential extinction rates between infaunal and epifaunal bivalves.

A variety of alternative causes should be examined to explain the increased infaunalization of Triassic bivalves. Perhaps most conspicuous are the differential environmental stresses (e.g., wave energy, salinity, oxygen deficiency, temperature) that exist in infaunal habitats compared to those at, and above, the sediment-water interface. Elevated environmental stresses for epifaunal habitats may be compounded by increased competition for space when compared to more stable three-dimensional infaunal habitats. Although this claim of epifaunal instability in infaunal versus epifaunal bivalves was rejected by Thayer (1974), who suggested that other factors, such as a taxon's geographic range, be considered, the argument for competition among benthic suspension feeders is still being debated (Sepkoski, 1996). Furthermore, the infaunalization may initially have been coordinated with the structure of biotic recovery following the end-Permian mass extinction. This hypothesis suggests that the differential extinction of epifaunal bivalves reflects the final elimination of epifaunal generalists that survived the end-Permian mass extinction. Several workers have commented on the relatively cosmopolitan opportunistic generalist bivalves that composed the Early and many Middle Triassic bivalve-dominated paleocommunities (e.g., Hallam, 1991; Schubert and Bottjer, 1995). Many of the Early Triassic bivalve survivors such as *Leptochondria* and *Myalina* and those with an essentially Permian flavor such as *Eumorphotis* were dominantly epifaunal. Such ecologic sorting after mass extinctions is now recognized as a common phenomenon following first- and second-order mass extinction (see the various references in Hart, 1996).

SUMMARY AND CONCLUSIONS

Following the end-Permian mass extinction, Triassic bivalves showed a gradual increase in generic richness during the Triassic and reached a peak number of 171 genera during the Carnian. Although the evidence for slow diversification may have been affected by preservational bias, the increase in generic richness was accompanied by an increase in the relative proportion of infaunal taxa. This infaunalization was due primarily to increased extinction rates for epifaunal genera. Origination rates for infaunal and epifaunal suspension-feeding bivalves were relatively similar.

The effects of predatory pressures in selective extinction have been hypothesized as a possible causal factor correlated to the increase of infaunalization during the Triassic. The trend of infaunalization persisted through the Triassic in spite of the lack of any clear evidence of shell drilling. These data question the assertion that the MMR was initially driven by predatory pressures or that many so-called predatory adaptations were in fact preadaptions, the origin of which can be found in a variety of ecological evolutionary processes that may be coordinated with the recovery from the end-Permian mass extinction.

REFERENCES CITED

Benton, M.J., 1986, More than one event in the Late Triassic mass extinction: Nature, v. 321, p. 857–861.

Carter, J.G., Barrera, E., and Tevesz, M.J.S., 1998, Thermal potential and mineralogical evolution in the Bivalvia (Mollusca): Journal of Paleontology, v. 72, p. 991–1010.

Fürsich, F.T., and Jablonski, D., 1984, Late Triassic naticid drillholes: Carnivorous gastropods gain a major adaptation but fail to radiate: Science, v. 224, p. 78–80.

Gradstein, F.M., Agterberg, F.P., Ogg, J.G., Hardenbol, J., Van Veen, P., Thierry, J., and Huang, Z., 1995, A Triassic, Jurassic and Cretaceous time scale, *in* Berggren, W.A., et al., eds., Geochronology, time scales and global correlation: SEPM (Society for Sedimentary Geology) Special Publication 54, p. 95–126.

Hallam, A., 1981, The end-Triassic bivalve extinction event: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 35, p. 1–44.

Hallam, A., 1991, Why was there a delayed radiation after the end-Palaeozoic extinctions?: Historical Biology, v. 5, p. 257–262.

Harper, E.M., Forsythe, G.T.W., and Palmer, T., 1998, Taphonomy and the Mesozoic marine revolution: Preservation state masks the importance of boring predators: Palaios, v. 13, p. 352–360.

Hart, M.B., 1996, Biotic recovery from mass extinctions: Geological Society [London] Special Publication 102, 394 p.

Johnson, A., and Simms, M.J., 1989, The timing and cause of Late Triassic marine invertebrate extinctions: Evidence from scallops and crinoids, *in* Donovan, S.K., ed., Mass extinctions: Processes and evidence: London, Bellhaven, p. 174–194.

Kowalewski, M., Dulai, A., and Fürsich, F.T., 1998, A fossil record full of holes: The Phanerozoic history of drilling predation: Geology, v. 26, p. 1091–1094.

Massare, J.A., and Callaway, J.M., 1990, The affinities and ecology of Triassic ichthyosaurs: Geological Society of America Bulletin, v. 102, p. 409–416.

Mazin, J.M., and Pinna, G., 1993, Palaeoecology of the armoured placodonts: Paleontologia Lombarda, v. 2, p. 83–91.

McRoberts, C.A., 1996, Extinction and survivorship of bivalve genera from the European Triassic: Geological Society of America Abstracts with Programs, v. 28, no. 7, p. 430.

McRoberts, C.A., and Newton, C.R., 1995, Selective extinction among end-Triassic European bivalves: Geology, v. 23, p. 102–104.

Newton, C.R., 1983, Triassic origin of shell-boring gastropods: Geological Society of America Abstracts with Programs, v. 15, no. 6, p. 652.

Olsen, P.E., Shubin, N.H., and Anders, M.H., 1988, Triassic-Jurassic extinctions: Science, v. 241, p. 1358–1360.

Patterson, C., and Smith, A.B., 1987, Is the periodicity of extinctions a taxonomic artifact?: Nature, v. 330, p. 248–252.

Schubert, J.K., and Bottjer, D.L., 1995, Aftermath of the Permian-Triassic mass extinction event: Paleoecology of Lower Triassic carbonates in the western USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 116, p. 1–39.

Sepkoski, J.J., Jr., 1981, A factor analytic description of the Phanerozoic marine fossil record: Paleobiology, v. 7, p. 36–53.

Sepkoski, J.J., Jr., 1987, Is the periodicity of extinctions a taxonomic artifact?: Reply: Nature, v. 330, p. 251–252.

Sepkoski, J.J., Jr., 1996, Competition in macroevolution: The double wedge revisited, *in* Jablonski, D., et al., eds., Evolutionary paleobiology: Chicago, University of Chicago Press, p. 211–255.

Stanley, S.M., 1968, Post-Paleozoic adaptive radiation of infaunal bivalve molluscs—A consequence of mantle fusion and siphon formation: Journal of Paleontology, v. 42, p. 214–229.

Stanley, S.M., 1977, Trends, rates, and patterns of evolution in the Bivalvia, *in* Hallam, A., ed., Patterns of evolution as illustrated by the fossil record: Amsterdam, Elsevier, p. 209–250.

Thayer, C.W., 1974, Environmental and evolutionary stability in bivalve mollusks: Science, v. 186, p. 828–830.

Thayer, C.W., 1979, Biological bulldozers and the evolution of marine benthic communities: Science, v. 203, p. 458–461.

Vermeij, G.J., 1977, The Mesozoic marine revolution: Evidence from snails, predators and grazers: Paleobiology, v. 3, p. 245–258.

Vermeij, G.J., 1987, Evolution and escalation, an ecological history of life: Princeton, New Jersey, Princeton University Press, 527 p.

Printed in USA