Evolutionary Rates and Patterns Among Cretaceous Bivalvia

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Analyses of over 100 lineages of Cretaceous Mollusca, primarily Bivalvia, representing diverse levels of morphological complexity, habitats, and adaptive strategies, clearly show that evolutionary rates (new taxa/unit time; or average taxa duration) vary widely *within* lineages subjected to changing environmental stresses, and *between* lineages and/or adaptive strategies subjected to broadly similar sets of environmental parameters through time. Modes of evolution range from gradualistic to punctuated, dependent upon rates and intensity of change in stress, or on levels of ecological opportunity (available ecospace). Extremely rapid rates of species evolution (one sp./0.08 Ma) and abrupt appearance of higher taxa occur during rapid radiations into unoccupied ecospace, and/or during high stress situations affecting whole biotas during short time intervals (e.g. rapid marine regression). Classification and reconstruction of molluscan phylogeny is most difficult over these intervals of geological time. Ecological factors far outweigh purely genetic factors in determining evolutionary rates and patterns among Mollusca, as determined by tests applied to Cretaceous lineages.

Phylogenetic reconstructions of molluscan lineages by means of the extant fossil record reveal a vast array of evolutionary patterns, representing broad variations in evolutionary rates. The systematic treatment and evolutionary interpretation of any group is highly dependent upon detailed knowledge of factors which cause these variations, their limits, and the extent to which rates and patterns of evolution are predictable. Our theoretical heritage teaches us to seek gradualistic sequences of evolutionary events linking phylogenetic end points, and to speculate on 'missing links' and stratigraphic omissions when such sequences are not found. Modern theory and observations, however, suggest that anything is possible.

Evolutionary patterns among marine invertebrate studied in continuous stratigraphic sequences may range from gradualistic (Kauffman 1970, fig. 4; Ozawa 1975), through mosaic or reticulate (Sylvester-Bradley 1977), to punctuated or stepwise in nature (Eldredge & Gould 1972, 1977; Gould & Eldredge 1977). Evolutionary rates range from extremely rapid (e.g. among ammonites and certain epifaunal bivalves: Kauffman 1970, 1972, 1977a) to extremely slow (e.g. in freshwater bivalves: Kauffman 1977a). Further, evolutionary rates may change dramatically *within* single lineages subjected to varying stress levels through time, and vary widely *between* co-occurring lineages subjected to similar sets of changing environmental parameters. Given the same set of environmental conditions, rates and patterns may be quite different for different taxonomic levels within the same group, e.g. species-level changes may be slow and gradualistic whereas generic and familial level changes may be abrupt or punctuated.

Whereas the chore of the evolutionary systematist and phylogenist was perhaps easier when theory predicted only slow, gradualistic evolution at all levels (e.g. the often quoted 1 species/Ma in lineages of invertebrates), the tremendous complexity of modern data makes it more

challenging, and more objective. We must accept phylogenetic discontinuity – the abrupt derivation of taxa within short periods of time – as a natural phenomenon, fully explainable, and revel in the ease at which we can classify such taxa. At the same time, evidence for gradualistic evolution exists in the fossil record (see Kauffman 1970, fig. 4; Ozawa 1975; discussion in Gould & Eldredge 1977), creating problems of defining boundaries between the taxonomic end points of a morphological continuum, but leaving little doubt as to phylogenetic relationships. We should view the entire range of debates between proponents of one phylogenetic interpretation against another, between slow and rapid evolutionary rates calculated for the same organisms, or between the gradualists and the punctuated evolutionists, in perspective. These are hypotheses partially subject to the vagaries of the fossil record and the individual scientist. Even the best examples of punctuated evolution (see, for example, Eldredge 1972) could, in theory, turn into gradualistic series with even closer stratigraphic collections of populations and greater geographic continuity of sampling. Calculated rates of evolution can also vary depending upon interpretation of the taxonomic units used for any lineage, and these may vary widely between workers studying the same lineages.

Yet, some consistency in rates and patterns of evolution is arising from multiple analyses of many different groups of organisms, and thus predictive ability is being gained from which to valuate phylogenetic interpretations and systems of classification (e.g. Kauffman 1970, 1972, 1977 a, for Cretaceous molluscs).

Perhaps the greatest amount of research into evolutionary rates and patterns among invertebrates has dealt with Mollusca, and in particular bivalves and ammonoids. Whereas this work is still in its early stages of development, initial results incontrovertably demonstrate broad variations in evolutionary rates and patterns which are closely tied to environmental fluctuations and changes in stress levels. The old image of the bivalve as a slowly and steadily evolving, simple invertebrate to be compared with the structurally complex, rapidly evolving Cainozoic mammals (see, for example, Simpson 1944, 1953; Stanley 1973) has little basis in fact at lower taxonomic levels. Bivalve and ammonite species and genera evolve as rapidly, and under the same broad sets of natural selective controls, as do any metazoans *yet measured against a real-time (radiometric) scale*. Measured rates of speciation within single Upper Cretaceous ammonite and bivalve lineages approach one species per 0.1–0.2 Ma, with individual species durations commonly ranging between 0.1 and 0.33 Ma and less commonly as low as 0.06–0.1 Ma (Kauffman 1970, 1972, 1977 a; this paper); these compare favourably with those cited for Late Cainozoic mammals.

The challenge that faces the palaeontologist–evolutionist in this field is obvious. If the extensive data that we are now collecting ultimately demonstrate that particular kinds of organisms representing certain adaptive strategies, trophic or habitat groups, levels of eurytopy *v*. stenotopy, levels of morphologic or genetic complexity and/or variability, etc., show broadly predictable rates and patterns of evolution under known sets of environmental factors, we are presented with a powerful tool in evolutionary systematics and phylogenetic reconstruction. If we can anticipate the 'tempo and mode of evolution' in a group of organisms, we can formulate hypotheses regarding their classification and expected phylogenetic patterns even before detailed analysis of that group. Such predictive ability not only allows discrimination of certain lineages or groups that are best qualified for testing evolutionary and ecological theory, or for application to biostratigraphy (Kauffman 1977 a), but it also allows identification of irregularities in the expected or 'normal' pattern of evolution which are of particular interest.

This study is concerned with evaluating controls on the rates and patterns of evolution in the Class Bivalvia by testing numerous Cretaceous lineages, representing diverse morphologies, habitat and trophic groups, levels of eurytopy, and other adaptive strategies, against several theories regarding factors influencing evolutionary rates. Preliminary work on selected lineages (Kauffman 1970, 1972, 1977 a) yielded encouraging results, but the quantity of data was too small to suggest conclusive relations. This study provides new data for many adaptive groups. All lineages studied come from the North American Interior and Gulf and Atlantic Coast Sub-provinces of the North American Province (see Kauffman 1973 a, 1978 b). This area was chosen specifically because of an excellent fossil record, which permits collection of closely spaced populations of diverse bivalves (see, for example, Kauffman 1970, fig. 4). Detailed interpretation of small to large scale environmental changes are also possible through careful stratigraphic analyses such as those of Hattin (1962, 1965, 1975). Finally, the most detailed radiometric time scale for the Cretaceous has been developed in the Western Interior from K–Ar dating of many of the 400–450 volcanic ash or bentonite beds found in this region (Gill & Cobban 1966; Obradovich & Cobban 1975; Kauffman 1978a, and references therein). These radiometric data provide the necesssary measure of species durations and evolutionary rates. Against this data base, more than 50 bivalve lineages have now been tested relative to numerous hypotheses regarding controlling factors on evolutionary rates and patterns in marine invertebrates.

Hypotheses regarding controls on evolutionary rates and patterns

In a preliminary study of Cretaceous bivalve and ammonite evolution, Kauffman (1977a) reviewed hypotheses put forth by various authors as to the factors controlling evolutionary rates and patterns, and tested these against limited numbers of lineages. To summarize, relevant theory is as follows:

(1) Evolutionary rates are related to genetic complexity, the number of loci on a genome, and the number of stages through which they can mutate (Haldane 1957, and subsequent authors). This is immeasurable in palaeontology; Mayr (1965) and Kauffman (1977a) present arguments why this is not a predictable relationship.

(2) Evolutionary rates are related to morphological complexity (a theoretical product of genetic complexity) (see, for example, Simpson 1944, 1953; Schopf, Raup, Gould & Simberloff 1975, using the number of discriminate morphological features without necessarily implying genetic complexity). This is subsequently tested within Cretaceous Bivalvia. Kauffman (1977a) provided data to suggest that this hypothesis is not valid when comparing marine vertebrates with various molluscs and with both planktonic and benthonic foraminiferans from the Western Interior Cretaceous seaway of North America. Slowest evolutionary rates were obtained from species of marine reptiles (the most complex organism) and benthonic foraminiferans (morphologically the simplest organism tested). The fastest evolutionary rates were obtained from ornate, morphologically complex ammonites and from morphologically simple epibenthic bivalves (Inoceramidae; Ostreidae). A broad spectrum of organisms gave intermediate values.

(3) Evolutionary rates are related to genetic variability within and between populations (Levinton 1973). This research has shown promising but inconclusive results suggesting relations between genetic variability in subpopulations, degree to which they are stressed, and potential for rapid evolution. If polymorphism, as reflected in population structure measured from hard parts, can be linked to genetic variability and heterozygosity, then a measure of

this factor could be made from palaeontological material; one would expect more rapid evolution in genetically variable, heterozygous, and/or polymorphic species within lineages.

(4) Evolutionary rates are related to trophic strategy, and thus the predictability of food resources (Levinton 1974; Kauffman 1977a). Trophic generalists would be expected to have more stable food resources, be less commonly stressed, and thus have longer species lives and slower evolutionary rates than trophic specialists. Levinton found this to be true in a preliminary comparison of mortality rates among selective suspension-feeding Pectinacea, Pteriacea, and Veneracea (mortality 1.2–1.5 % Ma^{-1}) and detritus-feeding Nuculoida (mortality 0.8 % Ma^{-1}). Kauffman (1977a) perceived the same relation for Cretaceous bivalves of North America; this test is considerably expanded here and subsequently discussed.

(5) Evolutionary rates are related to habitat characteristics and adaptive strategies within habitats. Levinton (1973, 1974) demonstrated that certain infaunal and deep water epifaunal bivalves had slower evolutionary rates than shallow water epifaunal bivalves because they lived in habitats which buffered them from high stress situations and large numbers of unpredictable environmental perturbations. Kauffman (1977a) similarly demonstrated this for certain Cretaceous bivalve lineages of North America. By assuming similar habitats for fossil taxa and living counterparts, based on physical occurrence and functional morphology, this theory can be widely tested in the fossil record.

(6) Evolutionary rates reflect degree of environmental tolerance, or eurytopy v. stenotopy, and thus stress levels for any single perturbation (Jackson, 1972, 1973; Levinton 1973, 1974; Kauffman 1970, 1972, 1977a). Stress in each case is measured by the degree to which environmental perturbations are unpredictable and thus lack programmed response within various groups. Predictably, different groups of organisms will react differently to the same perturbations in the environment they collectively occupy. Levinton's (1973, 1974) comparison of evolutionary rates in infaunal and epifaunal bivalves and between trophic groups is an indirect measure of this factor. More specifically, Jackson (1972, 1973) noted that species of tropical infaunal bivalves living in less than 1 m of water, where physico-chemical fluctuations were severe but predictable for resident taxa, evolved slower than counterpart taxa of the same groups living in shelf depths greater than 1 m, where major environmental fluctuations were less frequent but also much less predictable. Kauffman extended this study to test selected lineages of Cretaceous freshwater, intertidal, and brackish water molluscs against marine forms (1977a); slower evolutionary rates were shown by fresh, brackish, intertidal, and shallow subtidal marine organisms adapted to high levels of environmental fluctuation than by shelf-depth counterparts representing the same groups or adaptive strategies. Molluscs tested from environmentally variable habitats were more eurytopic, and less easily stressed than those from more stable offshore shelf environments.

(7) Evolutionary rates reflect intensity and rate of change of stress factors coupled with degree of eurytopy v. stenotopy. Kauffman (1970, 1972, 1977a) tested this hypothesis by measuring evolutionary rates in ecologically diverse Cretaceous marine molluscs during various stages of marine transgression (a time of ameliorating warming climates, expansion of ecospace, habitats and niche opportunities, and low levels of physico-chemical stress), and regression (a time of diminishing ecospace, size and diversity of niches, high biological competition, increasing turbidity, decreasing temperatures and salinity, increased seasonality, and increasing stress) in the Western Interior and Gulf Coast epicontinental seaways of North America (see figure 2). Highest evolutionary and extinction rates and decreasing diversity were found associated with

regressive (increasingly higher stress) periods; the more rapid the regression, the more rapid the rate of evolution and extinction. Within any marine regressive event, many stenotopic taxa became highly stressed and underwent rapid evolution and subsequent extinction with temperature and salinity changes at peak transgression and early in regression; moderately eurytopic taxa showed peak evolutionary rates near mid-regression, and most eurytopic taxa showed high levels of evolution only during late regression – results also predictable from Levinton's (1973, 1974) and Jackson's (1972, 1973) work. Data presented here support the hypothesis.

Hanley, Kauffman & Russell (1978) proposed different stress controls on evolutionary rates and patterns in North American fresh water molluscan lineages which relate to transgressive–regressive history of shelf and epicontinental seas. They propose that major periods of non-marine molluscan diversification might be broadly correlative with middle to peak phases of marine regression, when equitable maritime climates fostered by the wide spread of epicontinental seas were giving away to cooler and more seasonal climates (and thus increasing environmental stress) at the same time that prime ecospace for non-marine molluscs – wet coastal plain environments – were considerably expanding at the margins of retreating epicontinental seas. Conversely, they proposed (1978) that marine transgressive periods dominated by maritime climates on land and diminished width (but increased length) of coastal plain environments, were times of diminished non-marine molluscan radiation. Ecological opportunities were fewer and environmental stress lower during transgression. Data on four lineages of non-marine bivalves are presented here (figure 4*a*) which generally support the hypothesis.

8. Evolutionary rates reflect the rate and degree to which subpopulations are isolated, and size of isolated subpopulations (Mayr 1965; Eldredge & Gould 1972). Numerous studies of Quaternary to Recent organisms support this, but tests have not been widely made on older fossil material. The geological record provides the opportunity for such tests.

Whereas various other hypotheses exist, they are of lesser importance and not as clearly applicable to the study of fossil taxa. The tests applied here to Cretaceous Bivalvia primarily address themselves to hypotheses 2, rates *v.* morphological complexity; 4, rates *v.* trophic strategy; 5, rates *v.* habitat; and 6, rates *v.* degree of eurytopy or stenotopy shown by the group. Further, these data indirectly allow a test of hypothesis 7. In general, available hypotheses regarding controls on evolutionary rates and patterns fall into two conflicting schools of thought: (*a*) the primary controls are genetic, following Haldane (1967) and others; and (*b*) the primary controls are ecological, following Mayr (1965) and others. Recent studies suggest that (*b*) is most influential.

Measurement of evolutionary rates

Evolutionary rates have been evaluated in many ways, from purely subjective bases, through comparisons of taxa longevity based solely on their relative stratigraphic ranges, to purely analytical techniques employing a real-time radiometric scale (figure 1). The first two, upon which much inference has been made, are invalid in that the first has no measure of time, and the second depends upon too many natural variables becoming effective constants (e.g. sedimentation rate, continuity of sedimentation, preservation of the fossil record for different taxa, and at different times, etc.). At best the second method is a relative measure of differences in evolutionary rate, and then only when the total ranges of coexisting taxa are being compared.

A realistic measure of evolutionary rates can only be made against a radiometric (real-time) scale based on large amounts of data and close, relatively equal spacing of data points as in the

Pleistocene, and in the Western Interior Cretaceous sequences of North America (Gill & Cobban 1966; Obradovich & Cobban 1975; Kauffman 1977b, 1978a; and references therein). Accurate analysis of evolutionary rates also requires detailed, closely spaced palaeontological data (see, for example, Kauffman 1970, fig. 4), and some degree of constancy in the bases for systematic decisions (taxonomy) within each group being analysed. Finally, interpretation of evolutionary rates depends upon documentation of the changing environmental matrix
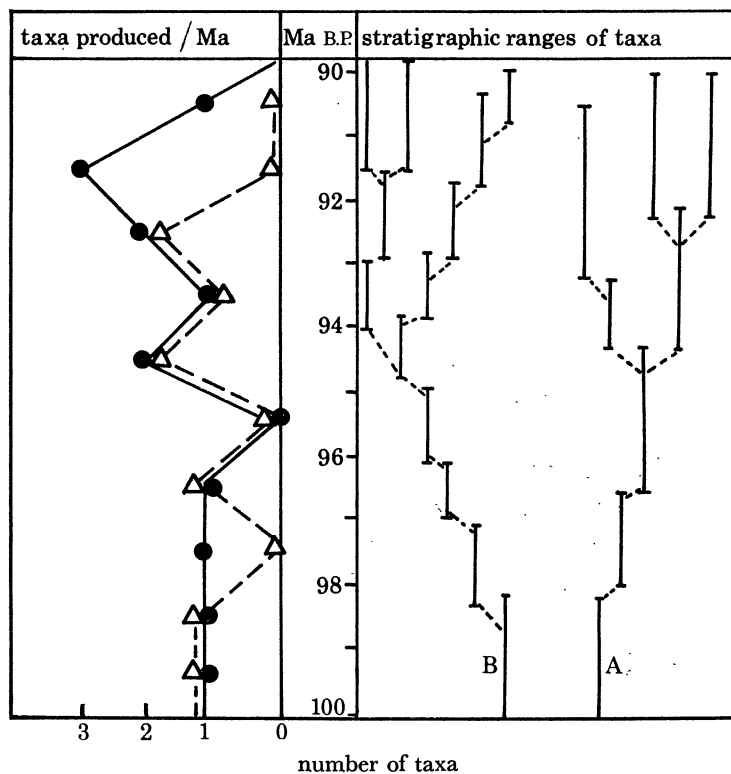

FIGURE 1. Models showing methods for measuring evolutionary rates from range zone data of fossil taxa, comprising the phylogenetic record of hypothetical lineages A and B (right), and measured against a radiometric scale (centre). Rates are calculated for both lineages by measuring individual species durations against the radiometric scale, totalling these durations for the entire lineage (15.9 Ma for lineage A and 16.2 Ma for lineage B), and dividing by the species number (8 and 13 respectively) to get an average species life duration (1.99 and 1.25 Ma respectively). Lineage B has the most rapid evolutionary rate. Figures 6 and 7 were prepared by this method. The left column shows curves for lineages A (△) and B (●) based on points which represent the number of new species appearing in each lineage per million year interval (figures 3–5 were prepared by this method). Dynamic variations in evolutionary rate, and spacing and magnitude of speciation episodes, are best shown in this way. Lineage B shows the highest rates of speciation, the highest single peak of speciation, and the most speciation events, all measures of evolutionary rate and magnitude.

(physical, chemical and ecological data) associated with lineage samples being analysed. All of these criteria can be met in the North American Cretaceous sequence (figure 2). The detail of the geochronological and environmental (stratigraphic) record is unexcelled in the Cretaceous anywhere, and through most of the Phanerozoic. Most of the lineages that have been analysed here and in past studies (Kauffman 1970, 1972, 1977a) have been systematically studied in recent years by one, rarely two, specialists so that there is a degree of constancy in taxonomic concepts for each lineage. Different workers have treated different lineages independently; thus the evolutionary rates observed do not reflect any single taxonomic philosophy.
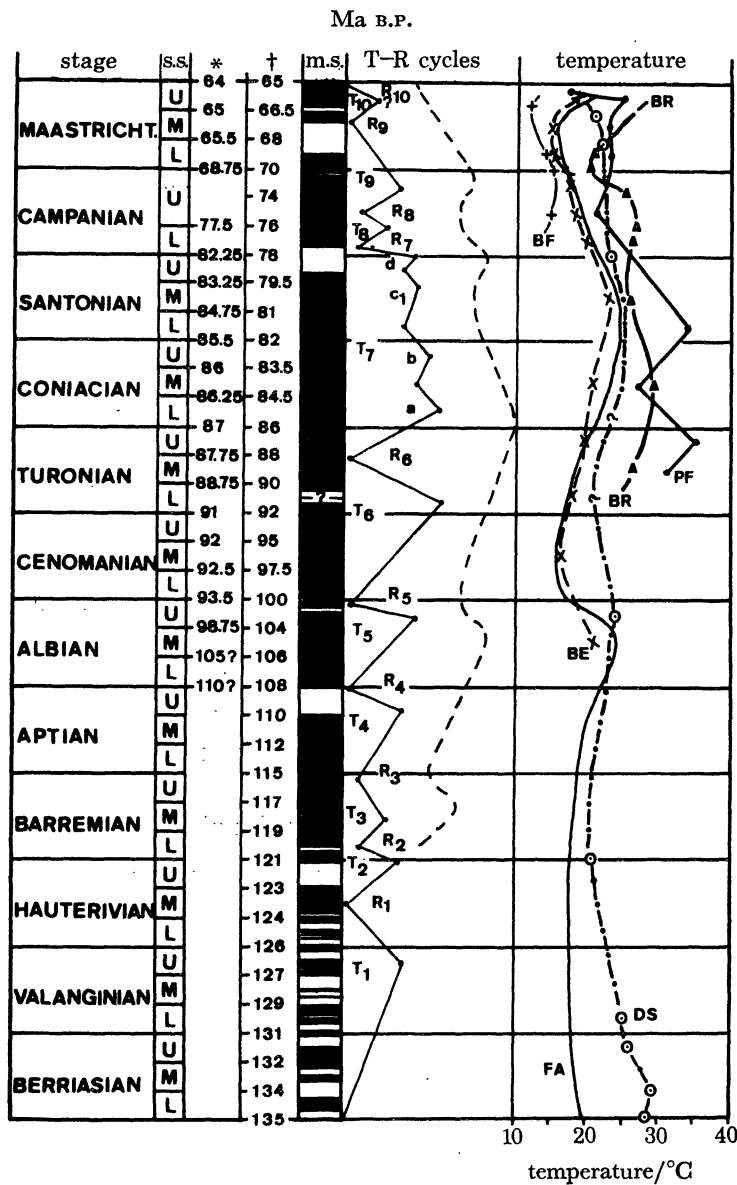
FIGURE 2. Cretaceous stages, substages (s.s.), generalized radiometric time scale for the Western Interior of North America (*) (Kauffman 1977 b) and averaged for the globe (†) by Van Hinte (1976), and magnetostratigraphy (m.s.) (Van Hinte 1976; black intervals normally polarized). Centre (T–R cycles) and right columns (temperature) show major environmental fluctuations affecting evolutionary rates and patterns of Cretaceous bivalves. Eustatic fluctuations are reflected by epicontinental transgressions (T_1–T_{10}) associated with eustatic rise (rising right slanted lines) and regressions (R_1–R_{10}; rising left slanted lines) with eustatic fall, both depicted by solid line in 'T–R cycles' column (Kauffman 1977 b); dashed line reflects broad global interpretation of eustasy by Schlanger & Jenkyns (1976). Temperature curves (right column, scale at bottom) based on oxygen and carbon isotopic analyses of diverse marine organisms (BR, brachiopods; BE, belemnites; BF, benthonic foraminiferans; PF, planktonic foraminiferans). Two generalized curves spanning the Cretaceous are from Frerichs & Adams (1973: FA), averaged from diverse data, and from Douglas & Savin (1973: DS) with the use of bulk samples and planktonic foraminiferans from the north central Pacific. Collectively, these data represent alternating low stress (transgressive and warming pulses, ameliorating climates) and increasingly higher stress conditions (epicontinental regression, cooling, climatic deterioration) which broadly affected the evolutionary rates and patterns of North American Cretaceous Bivalvia.

Having these data in hand, there are three common, yet distinct ways of measuring evolutionary rates:

(1) Measure average species life, or real-time duration, of all taxa within the lineage through all or a major part of its evolutionary history. This is normally done (figure 1) by taking the total range zone (all populations) of each species and measuring its real-time duration against a radiometric scale, and then compiling from these data an average taxon duration for the lineage. This method gives the best generalization of evolutionary rate, but unless small segments of the history of the lineage are analysed separately, the dynamic changes in evolutionary rates within the lineage are not clearly documented.

(2) Measure rate of production of new taxa (usually species) within the lineage. This is achieved (figure 1) by documenting the number of new taxa that originate within the lineage per unit real-time (usually per million years, measured radiometrically). This is a more vital measure of evolutionary rate within a lineage. It has the disadvantage, however, that when averaging taxa production rates over a long period of time for any lineage, the 'normal' production rate may be abnormally elevated by one or two major radiation events, as in the Cretaceous *Thyasira rostrata* lineage (figure 3c).

(3) Calculate mortality rate, the probability of a taxon becoming extinct within a certain time period, as applied by Levinton (1974). Survivorship curves, which measure the probability of a taxon surviving to a certain age (for a certain time duration), represent a similar but inverse measure. These methods, designed for the study of species populations, are more difficult to apply over long time periods, and less clearly depict the evolutionary history of a lineage than methods 1 and 2.

In the following analyses of Cretaceous bivalves from North America, methods 1 and 2 are both applied, and their results compared, in testing the various hypotheses concerning the controls on rates of evolution in marine invertebrates.

Studied Cretaceous lineages

Bivalve lineages were selected for this study to represent: (a) diverse morphologic complexity (from ornate heterodont Cardiidae to smooth edentulous Inoceramidae); (b) diverse trophic strategies (from generalized detritus feeders to specialized suspension feeders); (c) varied habitats (from fresh water to deep marine, and fully epifaunal to deep infaunal); and (d) varying degrees of eurytopy, or environmental tolerance (from cosmopolitan eurytopic Inoceramidae to endemic stenotopic Veneridae and Pectinidae). This diversity of adaptive types allows several of the hypotheses regarding controls on evolutionary rates to be tested, especially when added to data already published on bivalve lineages from the same areas by Kauffman (1970, 1972, 1977a).

In nearly every case, lineages were chosen for analysis only where phylogenetic relations were reasonably clear from close morphological similarities and/or actual population studies through time (e.g. in Inoceramidae of Kauffman (1970), fig. 4). The principal exception was within the genus *Nucula*, the sole representative of non-selective, semi-mobile detritus feeders with a good fossil record in the Western Interior and Gulf Coast Cretaceous sequences. Lineages of *Nucula*, as currently known, are very difficult to define and have not yet been determined. The data presented, therefore, represent all species of *Nucula* with a well known range zone in the North American Cretaceous; this naturally gives higher peaks in the graphs measuring evolutionary rates (figure 3a) than would result from individual lineage analysis.

The taxa analysed were taken from several modern monographic and/or large scale bio-stratigraphic works; usually one or two workers at most were responsible for systematic decisions within any one lineage, giving continuity to the data. Principal references employed for Gulf Coastal Plain bivalves were those of Stephenson (1941, 1947, 1952, 1955 *a*, *b*, 1956), Young (1963), and unpublished data on the Woodbine and Eagle Ford formations of E. G. Kauffman and J. D. Powell (personal communication, 1976). In the United States Western Interior, bivalve data were taken from Kauffman (1965, 1967, 1970, 1972, 1975, 1977 *a*, and works in press or in progress), Scott (1970), Twenhofel (1924), Speden (1970), Scott & Cobban (1966), Cobban & Reeside (1952), Hattin (1962, 1965, 1975), and Kauffman & Powell (1977). These data were supplemented by specific data from older works such as those of Stanton (1893), Meek (1876), and Whitfield (1880) and from numerous colleagues who have kindly contributed their expertise to this project. Revised range data from all Western Interior bivalve taxa used here will be presented in connection with a large study of Cretaceous biostratigraphy in the Western Interior United States and southern Canada (Kauffman & Cobban (eds) 1978) which is in the Geological Society of America Memoir series.

The lineages examined in this study are listed below in relation to the trophic or habitat groups in which they have been placed, based on examination *in situ* and/or research on the life habits of living counterparts. Data upon which the conclusions are presented appear in figures 3–7 and table 1. All lineages listed below were included in the test of morphological complexity *v.* evolutionary rates among Cretaceous Bivalvia.

In the test of trophic strategy and its possible relation to evolutionary rates, four major divisions of the studied lineages were made; all inhabited normal marine environments.

(1) Non-selective to broadly selective, sluggish burrowing detritus feeders, including all species of Cretaceous *Nucula* from the Gulf Coast and the Western Interior (figure 3 *a*). Lineages could not clearly be differentiated, and the data had to be aggregated, giving higher than normal readings for lineage analyses (figure 3 *a*). Species used were *Nucula* (*s.l.*) *catherina* Cragin, *N. rivulana* Stephenson, *N. sholsa* Stephenson, *N. nokonis* Adkins, *N. amica* Gardner, *N. micro-concentrica* Wade, *N. athabascensis* McLearn, *N. bellastriata* White, *N. haydeni* Shumard, *N. cancellata* Meek and Hayden, *N. microstriata* Gardner, *N. ciboloensis* Stephenson, *N. chatfieldensis* Stephenson, *N. nacatochana* Stephenson, *N. coloradoensis* Stanton, and *N. dowlingi* McLearn.

(2) Detritus feeders whose living representatives are commonly selective of particle type and/or size, and commonly more mobile in the substrate than (*a*) (figure 3 *b*). Lineages analysed are the *Nuculana mutata* Stephenson – *N. corsicana* Stephenson – *N. coloradoensis* Stephenson – *N. scitula* (Meek and Hayden) lineage; the *Yoldia microdonta* Meek – *Y. septariana* Cragin – *Y. subelliptica* Stanton – *Y. evansi* Meek and Hayden lineage; the '*Tellina*' (*s.l.*) *stabulina* Stephenson – *T. modesta* Meek – *T. munda* Stephenson lineage (figure 3 *b*). The *Protodonax oblongus* (Stanton) lineage (figure 4 *b*) questionably represents a part-time detritus feeding group.

(3) Suspension feeders which are relatively non-selective as to particle size and food type, and which have reduced particle sorting mechanisms (see Allen 1958; Kauffman 1967), such as (figure 3 *c*) the *Thyasira rostrata* Kauffman and *T. advena* – *T. becca* Kauffman (1967) lineages and the *Nymphalucina occidentalis* (Morton) lineage.

(4) Selective marine suspension feeders, including lineages of: deep infaunal *Pholadomya*, *Leptosolen*, *Panope*, *Legumen*, and *Solemya* (figure 5 *b*); moderately deep infaunal *Cymbophora*, *Linearia*, *Cyprimeria*, *Dosiniopsis*, *Crassatella*, and *Callistina* (figure 3 *d*); shallow infaunal *Protocardia*, *Trachycardium*, '*Cardium*' *pauperculum* Meek lineage, *Granocardium* (*Ethmocardium*), *Geltena*, and

Isocardia (figure 5a); largely exposed semi-infaunal lineages of *Pinna* and *Modiolus* (figure 4d); slightly exposed semi-infaunal lineages of *Idonearca* and *Breviarca*; deep-water epifaunal lineages of *Syncyclonema*, *Camptonectes*, *Pycnodonte* (small delicate encrusting forms) and *Platyceramus* (figure 5d); and shallower water epifaunal lineages of *Inoceramus*, *Mytiloides*, *Cremnoceramus*, *Sphenoceramus*, *Endocostea*, *Texigryphaea*, *Exogyra*, *Lopha*, and *Phelopteria* (figure 5c).

In related tests of habitat strategies, relative degree of shielding from environmental perturbations, degree of tolerance for environmental stress (eurytopy *v.* stenotopy) and evolutionary rates, nine divisions of the lineage data were made and compared; all taxa were selective suspension feeders except possibly *Protodonax* (partial detritus feeder?) so that trophic strategy is kept as constant as possible.

(1) Freshwater lineages of Unionidae, including Cretaceous North American representatives of *Protelliptio*, *Plesielliptio*, *Proparreysia*, and *Anodonta* (figure 4a). These range durations have been recently summarized by Hanley *et al.* (1978).

(2) Brackish water taxa including the *Brachidontes filisculptus* (Cragin) and *Crassostrea soleniscus* (Meek) lineages of the Gulf Coast and Western Interior (figure 4c); both mainly occur in estuarine and lagoonal deposits, and have precise modern counterparts in estuaries like Chesapeake Bay.

(3) Intertidal bivalves; data are taken from a single lineage, that of *Protodonax oblongus* (Stanton) as monographed by Vokes (1945). Shell morphology of these taxa suggests adaptation to intertidal environments as in modern *Donax*; some may have been subtidal as well. Evolutionary rates obtained from these taxa (figure 4b; discussed later) are faster than predicted by Jackson's hypothesis on evolutionary rates in intertidal and shallow subtidal environments (1972, 1973). Additional intertidal taxa, mainly gastropods and *Mytilus*, should be tested before conclusive statements regarding evolutionary rates in this physically variable environment can be made.

(4) Shallow water, shelf depth, epifaunal suspension-feeding bivalves including the following lineages (figure 5c): among Inoceramidae the *Inoceramus pictus* Sowerby – *I. cuvieri* Sowerby lineage, *Mytiloides labiatus* (Schlotheim) lineage, *Cremnoceramus deformis* (Meek) lineage, *Sphenoceramus lingua* (Goldfuss) lineage, and *Endocostea baltica* (Böhm) lineage; among Ostreidae the *Lopha lugubris* (Conrad) and *L. subovata* (Shumard) lineages, the *Texigryphaea corrugata* (Say) lineage, *Exogyra columbella* Meek lineage, and the *Phelopteria gastrodes* (Meek) lineage (Pteriidae). Habitats range from cemented, through epibyssate, to free living benthos.

(5) Deep water (middle to outer shelf depth) epifaunal bivalves including the *Syncyclonema simplicius* (Conrad), *Camptonectes platessa* (White), the *Pycnodonte newberryi* (Stanton) – *P. vesicularis* (Lamarck), and *Platyceramus platinus* (Logan) – *P. cycloides* (Wegner) lineages (figure 5d). Some of these have taxa which range into shallower water but all are more characteristic of offshore paleocommunities.

(6) Semi-infaunal taxa (figure 4d) including the *Pinna petrina* White and *Modiolus* (= *Volsella*) *tarrantana* Stephenson – *M. meeki* (Evans and Shumard) lineages, both of which are one-third to one-half exposed commonly in life, and the more deeply buried *Idonearca blanpiedi* Stephenson – *I. capax* Conrad and *Breviarca habita* Stephenson – *B. plummeri* Stephenson lineages which are essentially very shallow infaunal bivalves with the posterior flank commonly exposed at the sediment–water interface.

(7) Shallow burrowing infaunal bivalves, most of which have short siphons or none at all (figure 5a). This group includes the *Protocardia texana* (Conrad) – *P. hillana* Sowerby lineage

(exclusive of the unstudied *P. rara* Evans and Shumard plexus, 13 Ma in duration), the *Trachycardium tinninense* Stephenson – *T. eufaulense* Conrad lineage, the '*Cardium*' (gen.nov.) *pauperculum* Meek lineage, the *Granocardium* (*Ethmocardium*) *tippanum* Conrad lineage, the *Geltena obesa* Stephenson – *G. nitida* Stephenson lineage, and the *Isocardia slatana* Stephenson lineage.

(8) Moderately deep-burrowing infaunal bivalves, including the following lineages (figure 3*d*): The *Cymbophora emmonsi* (Meek) – *C. securis* Stephenson lineage, the *Linearia concentrica* Stephenson – *L. formosa* Meek and Hayden lineage, the *Cyprimeria alta* Conrad – *C. depressa* Conrad lineage, the *Callista* (*Dosiniopsis*) *orbiculata* Hall and Meek – *C* (*D.*) *owenana* Meek and Hayden lineage, the *Crassatella vadosa* Morton lineage, and the *Callistina lamarensis* (Shumard) lineage.

(9) Deep burrowing infaunal taxa, including the following lineages (figure 5*b*): The *Panope subparallela* Shumard – *P. subplicata* Shumard lineage, the *Leptosolen biplicatus* Conrad – *L. angustus* Stephenson lineage, the *Pholadomya belviderensis* Twenhofel – *P. goldenensis* Stephenson – *P. coloradoensis* Stanton lineage, the *Legumen ellipticum* Conrad lineage, and the *Solemya bilix* White – *S. subplicata* Meek and Hayden lineage.

Whereas many other lineages are currently under investigation, these data provide a fair test of various theories regarding rates and patterns of evolution in Cretaceous bivalve molluscs at the species level.

Analyses of data

Figures 3–7 allow four types of analyses of evolutionary rates among North American Cretaceous Bivalvia, representing diverse ecological strategies and morphological types. The data are summarized in table 1.

(1) In figures 3–5 the number of species generated within lineages per million year interval are documented as one measure of evolutionary rate to be tested against different trophic, habitat, or morphological complexity groups. The highest peaks represent the most rapid rate of species production. Note that for most lineages, rates vary considerably through time; speciation peaks are separated by intervals with little or no speciation. This is a normal pattern in molluscan evolution during the Mesozoic (see, for example, Kauffman 1970, 1972, 1977*a*) and mainly reflects changes in stress levels with fluctuating marine and continental environments.

(2) Figures 3–5 also provide data for testing evolutionary rates as a function of varying stress levels, environmental tolerance (degree of eurytopy) and ecological strategies associated with principal fluctuations in North American marine environments. These fluctuations mainly resulted from a global eustatic changes producing transgressions (T) and regressions (R) in shelf and epicontinental areas, representing alternating low and high stress conditions respectively (previous discussion). Kauffman (1970, 1972, 1977*a*) proposed that regressions should produce more rapid rates of evolution, higher levels of extinction, and generally lower diversity among marine organisms than should transgressions. Exceptions would be among groups preadapted to niches newly opened during transgression, or groups of ecological opportunists biologically stressed by competition from better adapted stenotopes during transgressive succession. Figures 3–5 show, at the top of each, the transgressive–regressive history of epicontinental and shelf seas in North America and elsewhere, after the global scheme of Kauffman (1970, 1973*a*, *b*, 1977*b*, 1978*b*). Thus T_5–T_{10} represent periods of eustatic rise and widespread transgression onto many world epicontinental areas, and R_5–R_{10} represent equally widespread regressions. Hypotheses suggesting that increased rates of evolution are associated with

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increased stress levels during regression can be tested by comparing times of peak evolutionary rates, and/or the distribution of speciation events, for any lineage with the transgressive–regressive history shown at the top of figures 3–5.

(3) Figures 3–5 can also be used to test diverse hypotheses concerned evolutionary rates and patterns by observing the *number* of important diversification (speciation) events during the history of the lineage, and comparing these between lineages of different morphological complexity, habitats, trophic strategies, and environmental tolerance (level of eurytopy).
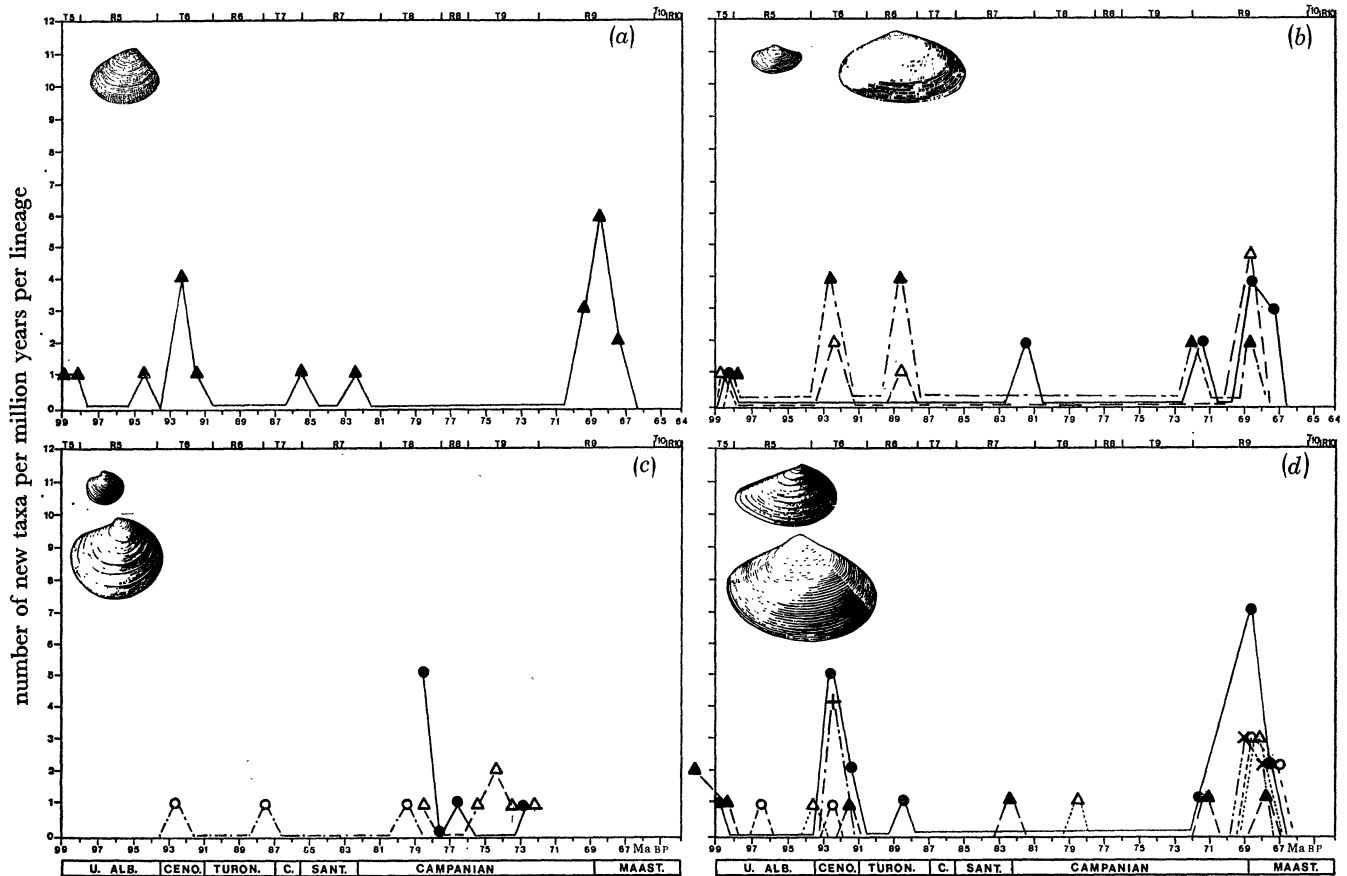

FIGURE 3. Evolutionary rates of four trophic groups of Cretaceous Bivalvia from North America, as documented by plotting the number of new species and/or subspecies arising within each lineage per million year interval, measured radiometrically (see Obradovich & Cobban 1975; Kauffman 1977 b, 1978 a). Each lineage is represented by a different symbol, explained below. Plots also show peak speciation levels attained by each group, number of speciation episodes for each group, and regularity of speciation events. Data are summarized in table 1 and interpreted in the text. (a) Plot of all species of *Nucula* (▲), *without attempting to recognize lineages*, representing slow burrowing to nearly stationary, non-selective detritus (deposit)-feeding Bivalvia. (b) Plots for three lineages of mobile, selective detritus (deposit)-feeding Bivalvia of the genera *Nuculana* (●), *Yoldia* (△), and '*Tellina*' s.l. (▲); lineages described in the text. The intertidal bivalve *Protodonax* (figure 4b) represents another selective detritus feeder with comparable data. (c) Plots for three lineages of non-selective infaunal suspension (filter) feeding Bivalvia with reduced particle sorting structures. Lineages are: ●, *Thyasira rostrata*; △, *Thyasira becca-advena*; ○, *Nymphalucina occidentalis*. Note generally low levels of evolution except for single 'middle' Campanian burst of speciation and subspeciation in *T. rostrata* lineage with initial development of its preferred habitat, and its first immigration and radiation into the Western Interior epicontinental seaway (Kauffman 1967) on transgression 8. (d) Plots for six lineages (described in the text) of moderately deep burrowing, infaunal, selective suspension (filter) feeding Bivalvia: ●, *Cymbophora*; ○, *Linearia*; ▲, *Cyprimeria*; △, *Callista* (*Dosiniopsis*); ×, *Crassatella*; +, *Callistina*. Note the general trend toward higher and more numerous speciation events among selective suspension feeders than among other groups of trophic generalists (discussion in text).

(4) Figures 6 and 7 provide a different test for evolutionary rates and patterns among Cretaceous bivalves. These figures present data on the average species life, or time-stratigraphic duration, for all lineages analysed from each trophic strategy (figure 6) or habitat group (figure 7), as a test of the relations of these ecological factors to evolutionary rates. Each point on each group represents the *average species life* for one lineage throughout its known fossil record in North America. The mean value of all data points for each habitat or trophic group is also shown and lines are fitted to these points. The ensuing interpretations of factors influencing evolutionary rates in Bivalvia depend heavily upon these graphs.

Whereas figures 6 and 7, and an analysis of numbers and position of evolutionary peaks *v.* marine eustatic history in figures 3–5, give the best general view of evolutionary relations to ecological and environmental factors, the dynamics of evolution within individual lineages are

TABLE 1

habitat or trophic strategy (1)	average species duration Ma (2)		average:highest speciation rate per lineage (species/Ma) (T or R)† (3)		average no. of speciation events (4)		average species production rate for speciation events only (species/Ma) (5)		average species production rate for duration of lineage (species/Ma) (6)		no. of speciation events on T v. R pulses (7)	
	a	b	a	b	a	b	a	b	a	b	T	R
evolutionary rates v. trophic strategy												
n.s.d.f.	3.03	3.03	6.0 R	6.0	10.0	10.0	2.1	2.1	0.62	0.62	4	6
s.d.f.	2.5	2.2	4.3 R	4.0	4.67	5.5	2.42	2.25	0.36	0.44	6	8
n.s.s.f.	2.8	2.8	2.67 T	2.67	3.67	3.67	1.51	1.51	0.69	0.69	10	1
s.s.f.i.	2.13	2.64	2.71 R	2.81	3.65	3.67	1.8	1.82	0.6	0.56	34	47
s.s.f.e.	1.25	2.0	4.3 R	3.8	4.3	4.43	2.36	2.09	1.59	1.1	25	20
evolutionary rates v. habitat strategy‡												
f.w.	5.63		3.25 R		3.8		1.9		0.37		6	8
b.w.	3.17		2.0 T		5.0		1.2		0.17		5	5
int.	1.3		3.0 R		8.0		1.75		0.67		4	5
sh.e.	1.25		4.3 R		4.3		2.36		1.59		25	20
sh.s.i.	1.81		3.0 R		5.0		1.44		0.32		7	12
sh.sha.i.	2.04		2.8 R		3.3		1.9		0.8		9	11
sh.m.d.i.	2.08		3.7 R		3.8		2.3		0.8		9	14
sh.d.i.	2.28		1.4 R		3.8		1.13		0.17		9	10
d.w.e.	3.3		2.5 R		4.75		1.85		0.36		10	9
morphological complexity group	*evolutionary rates v. morphological complexity*											
5 (complex)	2.19		3.8 R		4.17		1.95		0.5			
4	2.95		3.56 R		4.89		2.02		0.69			
3	1.88		3.42 R		3.75		2.09		0.74			
2	2.45		2.79 R		4.21		1.72		0.81			
1 (simple)	2.72		2.88 T		4.88		1.64		0.83			

Notes: b.w., brackish water; d.w.e., deep water epifauna; f.w., freshwater; int., intertidal; n.s.d.f., non-selective detritus feeder; n.s.s.f., non-selective suspension feeder; s.d.f., selective detritus feeder; sh.d.i., deep burrowing infauna, shelf zone; sh.e., shelf epifauna; sh.m.d.i., moderately deep burrowing infauna, shelf zone; sh.sha.i., shallow burrowing infauna, shelf zone; sh.s.i., semi-infaunal habitat, shelf zone; s.s.f.i., selective suspension feeder, infaunal; s.s.f.e., selective suspension feeder, epifaunal. In all cases, column *a* represents data only from normal marine shelf habitats, and column *b* data from all sources for each ecological grouping.

All data in million year intervals, measured radiometrically. Column numbers refer to citations in the text.

† T, events during transgressive marine pulses; R, events during regressive marine pulses.

‡ All selective suspension feeders except int.

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best shown in biological data presented in figures 3–5. The same lineages are analysed in figures 3–5 as are used as the bases for figures 6 and 7, providing an independent check on the relations between evolutionary rates and patterns, environmental fluctuations, ecological and trophic strategies, and morphologic complexity.
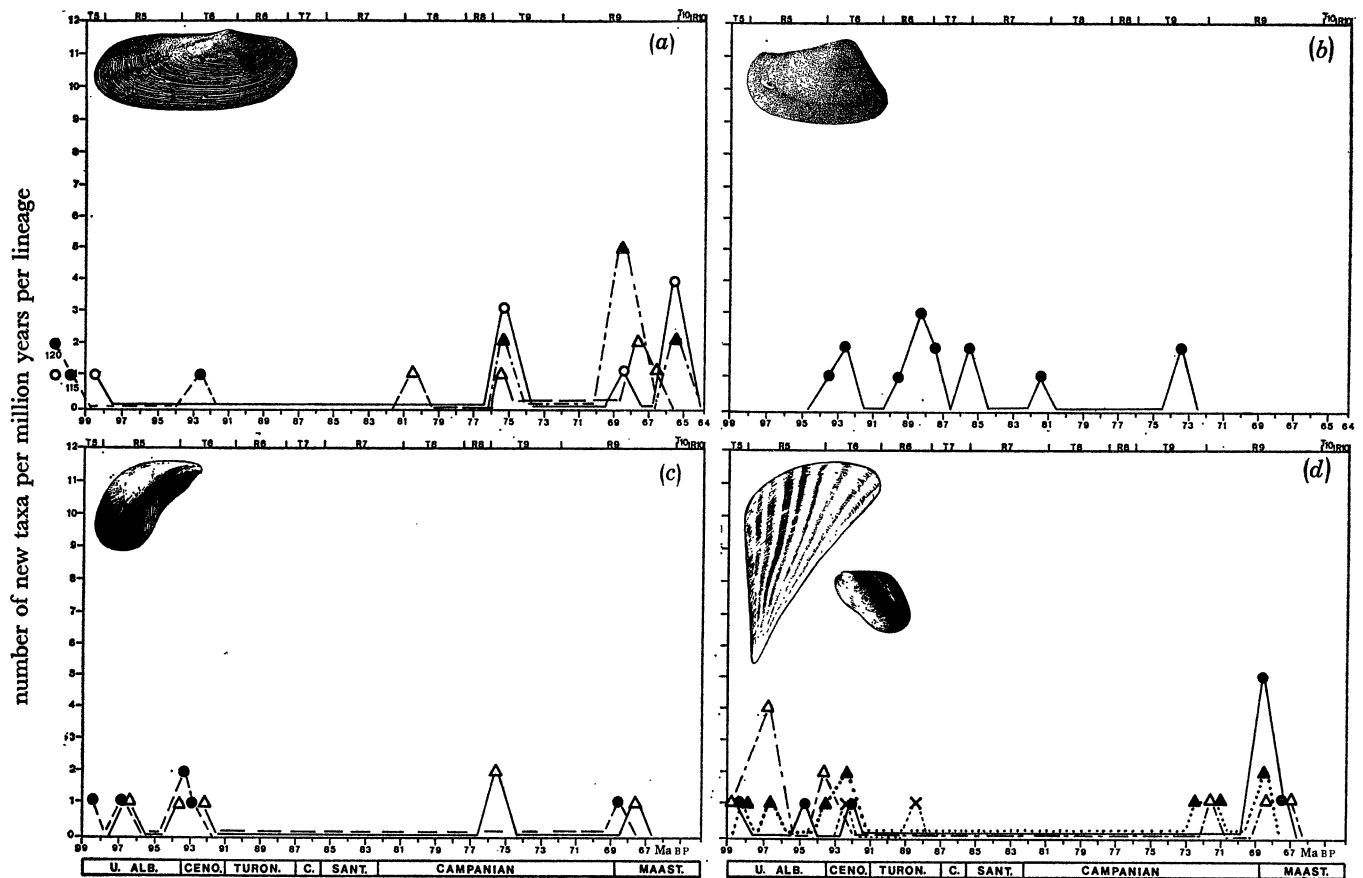

FIGURE 4. Evolutionary rates of North American Cretaceous Bivalvia from four distinct habitats (lineages defined in text), representing high (freshwater, brackish water, intertidal) to moderate (offshore marine semi-infaunal) levels of physical and chemical environmental variation. Rates measured by number of new species arising in each lineage per million year interval, measured radiometrically (Obradovich & Cobban 1975; Kauffman 1977 b, 1978 a; figure 2 herein). Lineages are differentiated by symbols explained below. Plots also show peak speciation levels for each lineage, number of speciation events per lineage, and regularity of events. Data are summarized in table 1 and interpreted in the text. (a)–(c) represent taxa with high, genetically derived tolerance for environmental fluctuations and thus low potential for frequent biological stress and rapid evolution (rates in Protodonax (b) higher than expected for intertidal organisms); (d) represents more stenotopic taxa of the marine shelf, subject to greater stress through environmental perturbation, and with greater potential for rapid evolution. (Figure 5 continues this comparison among normal marine Bivalvia.) (a) Freshwater lineages (●, Protelliptio; ○, Plesielliptio; ▲, Proparreysia; △, Anodonta) from the Western Interior United States and southern Canada, from Hanley et al. (1978); note major radiations in widespread, moist coastal plain environments developed during Upper Campanian regression. (b) Data from presumed intertidal bivalves of genus Protodonax (●) in the Western Interior and western Gulf Coast United States; data mainly from Vokes (1945). Note higher rates and peaks of evolution than predicted by Jackson's study of very shallow subtidal bivalves (1972, 1973). (c) Data from the two most common brackish water lineages in North America (●, Brachidontes filisculptus; △, Crassostrea soleniscus), showing predictably low evolutionary rates. (d) Data from moderately exposed (Pinna (×), Modiolus (▲)) and slightly exposed (Idonearca = Cucullaea, (●), Breviarca (△) semi-infaunal bivalves, Western Interior and western Gulf Coast U.S.A.
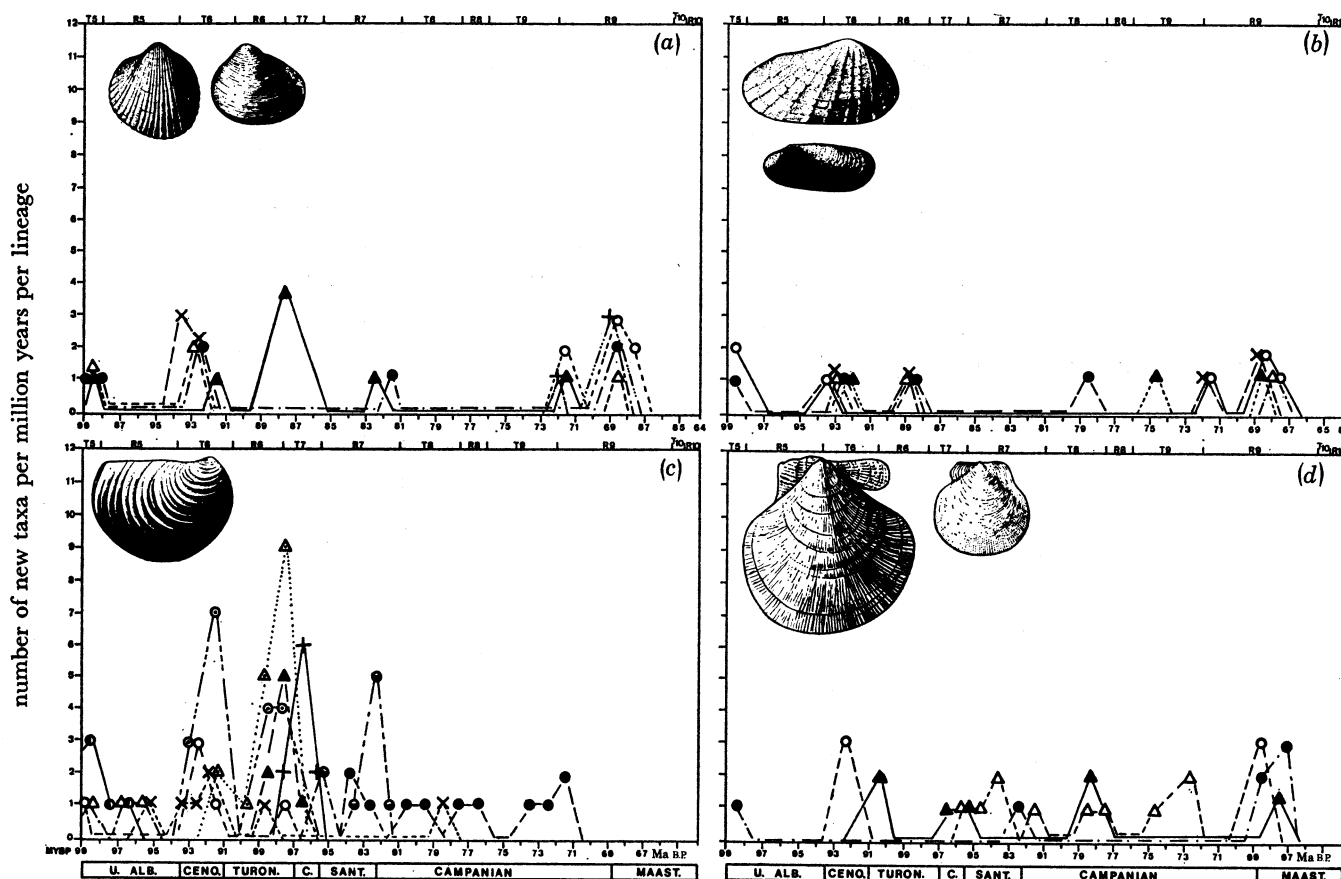
FIGURE 5. Evolutionary rates among North American Cretaceous Bivalvia, representing selective suspension feeding, normal marine groups with distinct habitat strategies (compare with data in figure 4). Rates measured by numbers of new species, subspecies, arising in each lineage per million year interval, measured radiometrically (see Obradovich & Cobban 1975; Kauffman 1977 b, 1978a; figure 2 herein). Lineages differentiated by symbols explained below and described in the text. Data are summarized in table 1 and interpreted in the text; these data used both for tests of evolutionary rate v. habitat strategy and rate v. trophic strategy (in combination with figure 3). (a) Plots for diverse, shallow-burrowing infaunal taxa from normal marine environments of shelf depth (●, Protocardia; △, Trachycardium; ▲, 'Cardium' pauperculum lineage; ○, Granocardium (Ethmocardium); ×, Geltena; +, Isocardia); note frequent but relatively moderate magnitude speciation events. (b) Plot of diverse, deep burrowing lineages from normal marine, shelf depth environments (●, Pholadomya; ○, Leptosolen; ▲, Panope; △, Legumen; ×, Solemya); note numerous but low level speciation events compared with more readily stressed, environmentally less protected lineages in (a) and (c). (c) Plots of evolutionary rate for diverse suspension feeding, marine, epifaunal bivalves living mainly at shelf depths (Lineages: ◐, Texigryphaea corrugata; ○, Exogyra columbella; ▲, Lopha lugubris; △, Lopha subovata; ×, Phelopteria gastrodes; ⊙, Inoceramus pictus– I. cuvieri; △, Mytiloides labiatus; +, Cremnoceramus deformis – C. inconstans; ◓, Sphenoceramus lingua; ●, Endocostea baltica); note frequent and high level speciation events in this, the most rapidly evolving habitat group. (d) Plots for diverse lineages of primarily deep water (outer shelf, slope depths; deep basinal habitats) suspension feeding epifaunal Bivalvia (●, Syncyclonema; ○, Camptonectes; ▲, Pycnodonte; △, Platyceramus); note frequent but moderately low level speciation events compared with shallow water epifauna, reflecting greater protection and environmental predictability of deeper water habitats.

EVOLUTIONARY TESTS

Evolutionary rates v. morphological complexity

In palaeontology, tests of hypotheses suggesting that evolutionary rates are dependent upon genetic complexity and variability, and thus potential rates of mutation and recombination to produce new structures, must translate into analyses of morphological complexity in

preserved hard parts. This is a poor measure at best. Nevertheless, several authors have suggested that morphologically complex fossil organisms such as Cainozoic mammals (representing complex genetic systems) evolved much faster than morphologically (genetically?) simpler organisms such as bivalves (see, for example, Simpson 1944, 1953; Stanley 1973; and references therein). Schopf *et al.* (1975) proposed that the number of morphological terms applied to the description of any taxon represents a measure of its morphological complexity, and produced a model in support of the contention that morphologically more complex organisms have faster evolutionary rates than morphologically simpler organisms. These authors rightly pointed out that this relation may be artificial to the extent that equally small genetic changes could be manifest in the morphology of complex organisms but not in simple organisms, and further
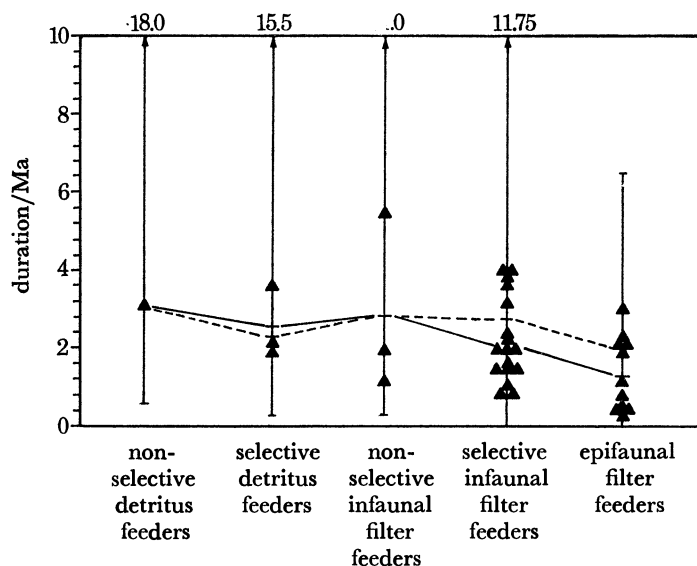

FIGURE 6. Evolutionary rates of North American Cretaceous bivalves representing a broad range of trophic strategies, from non-selective detritus (deposit) feeders to highly selective filter (suspension) feeders. Rates measured by calculating average species longevity for each lineage (▲) and connecting the mean values for all lineages within each trophic group with lines representing (*a*) normal marine bivalves from shelf-depth environments (solid line), and (*b*) all bivalves in each trophic group regardless of habitat (broken line). See the text for a discussion of differences. Vertical dark lines with numbers (in Ma) at top indicate spread of individual species durations recorded for each trophic group. Note that this spread decreases with increasing complexity in trophic strategy, and that within the marine shelf environment, average species duration decreases (evolutionary rates increase) from the least specialized to the most specialized trophic group.

that because of the diversity of obvious structures, morphologically complex fossil organisms may be more finely split taxonomically than simpler organisms, and thus superficially seem to have more rapid evolutionary rates. In this latter case, taxonomic philosophy rather than genetic complexity would be predominantly reflected by differences in 'evolutionary rates' between simple and complex organisms.

In opposition to this view, Mayr (1965) concluded that ecological factors were much more important than purely genetic factors in determining rates of evolution. Stanley (1973) also stressed ecological factors (especially competition) as contributing strongly to more rapid rates of evolution in mammals, and certain bivalves (rudists). Kauffman (1977a) tested this hypothesis by comparing radiometrically determined speciation rates and species durations among diverse Cretaceous marine organisms from the Western Interior United States. Marine reptiles

were compared with diverse molluscs and with both planktonic and benthonic foraminiferans in a graded series of morphological complexity. No relation was found between morphological complexity and evolutionary rates. Marine reptiles and benthonic foraminiferans showed the *slowest* evolutionary rates, planktonic foraminiferans and trophic generalist bivalves had the next slowest rates; specialized suspension feeding infaunal bivalves and gastropods showed moderately fast rates, and ammonites and epifaunal, morphologically simple bivalves (e.g. Inoceramidae) had the most rapid rates in this comparison. The fastest rates of evolution recorded among these molluscs (1 species/0.06–0.1 Ma in lineages) are comparable with the evolutionary rates recorded for Late Cainozoic mammals.
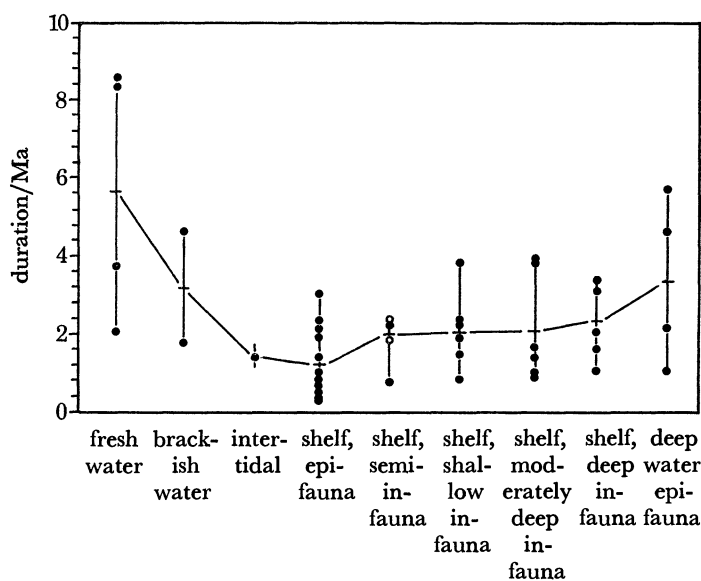

FIGURE 7. Evolutionary rates of North American Cretaceous Bivalvia, representing a broad range of habitat strategies and environmental tolerance (eurytopy *v.* stenotopy); see discussion in the text of relations between these factors. Each point represents the mean duration of species life within a single lineage. Among semi-infaunal bivalve lineages, those with moderate levels of exposure above the sediment surface (●) are differentiated from those that are mostly buried (○) to demonstrate that taxa which are more protected from environmental perturbations have generally slower evolutionary rates and longer-lived species. Species durations measured radiometrically from North American geochronology of Obradovich & Cobban (1975) and Kauffman (1977b, 1978a). The horizontal line connects mean values for all lineages in each habitat group. Note increasing evolutionary rates (decreasing average species durations) from freshwater to shallow marine habitats, depicting a close relationship between evolutionary rate and scope of environmental tolerance among bivalves. Note also declining evolutionary rates from intertidal and shallow water epifaunal lineages, through gradually deeper burial among shelf infaunal bivalves, to deeper water epifaunal bivalves. This trend reflects a close relationship between evolutionary rates and habitat strategy – or degree to which habitat protects populations from unpredictable environmental perturbations – and thus stress.

In the present study, a sufficient range of morphological complexity is present in bivalves chosen for analysis to test this hypothesis within a single taxonomic group. Four groups of morphological characters were studied on shells of each lineage and ranked as to their complexity (*a*) surface ornamentation; (*b*) major features of shell form such as presence or absence of auricles, folds, sulci, etc.; (*c*) dentition; and (*d*) musculature. For example, a rank of 5 was given to complex taxodont or heterodont, ornate bivalves with complex musculature and/or folds, sulci, auricles, etc. (e.g. Cardiidae, *Idonearca*); a rank of 4 was given to similar forms lacking complex shell form or ornament (e.g. *Nucula*); a rank of 3 was given to groups with simple

dentition, moderately complex musculature, and ornamented shells (or greatly reduced dentation, complex musculature, and ornamented shells) (e.g. *Brachidontes*, *Camptonectes*); a ranking of 2 was given to bivalves with greatly reduced or completely absent dentition, moderately simple musculature, and well ornamented or complex shells (e.g. *Mytiloides*, *Lopha*); and a ranking of 1 given to basically edentulous shells, with simple musculature and shell form, and lacking well defined external ornamentation (e.g. some *Inoceramus*, *Thyasira*). Values on evolutionary rates were then totalled and averaged for each morphological group (table 1) in the same manner as calculated for different trophic or habitat groups.

All but one of these tests show no relation between evolutionary rate and morphological complexity. Table 1 indicates no trends in average species duration within lineages (group 4 longest duration; group 3 shortest; table 1, column 2), no trends in the number of speciation events during the history of the lineage (groups 1, 4 highest, group 3 lowest; table 1, column 4), or in the average number of species produced within the lineage per speciation event (group 3 highest, group 1 lowest; table 1, column 5). Further, for the entire time span of each lineage studied, the average speciation rate (table 1, column 6) shows a constant but *inverse* relation to morphological complexity, with the highest rates in group 1, the lowest in group 5, and values graded between them.

The only apparent correlation between evolutionary rate and morphological complexity is in regard to the magnitude of the peak speciation rates recorded in the samples; *on the average*, the highest speciation peak for each lineage occurs in the most complex morphological group (5), and the lowest single speciation peaks occur in lineages belonging to the simplest group (1), with intervening values graded according to complexity (table 1). The significance of this apparent relation is hard to assess, in as much as the highest recorded speciation rates (8 species/ Ma) for any single lineage among all the data are in group 2 taxa (*Mytiloides labiatus* lineage) and the next highest recorded rates (6 and 7 species/Ma) are predominantly within complexity groups 1–3, with one example from group 4.

Thus the great majority of data suggest little or no correlation between evolutionary rates and morphological complexity among North American Cretaceous bivalve lineages. A general relation exists between morphological complexity and averaged values for the highest rate of species production recorded for each lineage in each complexity grouping (table 1, column 3), but this trend is not substantiated either by the occurrence of the highest recorded speciation rates among all individual lineages (in groups 1–4), by the distribution of the number of speciation events during the history of the lineage (table 1, column 4), in speciation events during the history of the lineage (table 1, column 4), in speciation rates calculated only for speciation events (table 1, column 5) or in speciation rates calculated over the entire time span of the studied lineage (table 1, column 6). These data support the theory of Mayr (1965) and confirm preliminary studies of Kauffman (1970, 1972, 1977a) on diverse marine organisms. We must therefore look to ecological factors for the principal controls on evolutionary rates and patterns; several tests follow.

Evolutionary rates v. trophic strategy

Trophic resources are a critical ecological factor in the successful adaptation of an organism to its environment. These resources fluctuate to varying degrees in the marine realm; to the degree that these fluctuations are unpredictable (e.g. non-cyclic), especially over short periods, they impose environmental stress on populations. As a generality, benthonic organic detritus

shows little or no short-term, unpredictable fluctuation, microplankton shows moderate numbers of unpredictable fluctuations, and macrofaunal prey organisms probably show the greatest fluctuations. Accordingly, environmental stress (and therefore evolutionary rates) in populations of macropredators would be expected to be greatest because of frequent, unpredictable perturbations in their trophic resources; stress on plankton suspension feeders would be moderate, rarely severe, and stress on detritus feeders would be lowest over long periods of geological time, theoretically leading to low rates of evolution. Intermediate trophic strategies would be expected to experience intermediate stress levels and evolutionary rates if this hypothetical relation exists, and other factors are held constant.

Levinton (1974) successfully tested the hypothesis that evolutionary rates among marine bivalves should vary according to their trophic strategy and the predictability of their food resources. More rapid evolutionary rates were calculated among genera of marine suspension feeding Pectinacea, Pteriacea, and Veneracea than among detritus feeding Nuculoida, as evidenced by appreciably lower mortality rates among the nuculoids. Kauffman (1977a) supported Levinton's findings in a preliminary study of Cretaceous molluscan lineages from the Western Interior United States. He found that specialized pelagic to epibenthic predators and suspension feeders (ammonites) and specialized (particle selective) epifaunal suspension feeding bivalves showed the fastest rates of evolution on the average, selective infaunal suspension feeders (bivalves, turritellid gastropods) the next fastest, generalized (less selective) infaunal suspension feeders (lucinacean bivalves) the next fastest, and detritus feeding infaunal bivalves the slowest evolutionary rates (nuculoids). These tests are expanded here and restricted to analysis of Bivalvia within fully marine shelf environments to provide some level of constancy among other important environmental factors. Kauffman's (1977a) data are here revised by addition of species data to lineages and slight revision of the radiometric scale used to measure evolutionary rates (Kauffman 1978a).

To test the hypothesis that trophic strategy is related to evolutionary rate, four trophic divisions of studied marine bivalve lineages were made. Division of deposit-feeding bivalves into *non-selective detritus feeders* and *selective detritus feeders* is suggested by the differential mobility and specialization among feeding structures between the two groups, and by the greater longevity of *Nucula* populations in single habitats also occupied by nuculanids and tellinids when that habitat is severely stressed. Suspension feeding bivalves are subdivided on the basis of differential specialization in the morphology of feeding structures and trophic behaviour. *Non-selective suspension feeders* (e.g. lucinaceans) have greatly reduced particle sorting mechanisms (Allen 1958; Kauffman 1967). *Selective suspension feeding bivalves* with complex particle sorting and transport structures are subdivided in this test into infaunal and epifaunal groups, which generally show higher specialization in feeding and particle sorting structures, especially on the mantle. Obvious differences in evolutionary rates between infaunal and epifaunal selective suspension feeders (figure 6), however, may reflect differences in habitat protection (less for epifauna) more than slight differences in trophic specialization (discussed later).

Evolutionary rates as determined (a) by number of species generated within lineages per million year interval, (b) by peak levels of speciation obtained, and (c) by number of speciation episodes per unit time are graphed in figure 3 for groups of detritus-feeding and infaunal suspension feeding Cretaceous bivalves, and in figure 5 for epifaunal and additional infaunal taxa of normal marine, shelf-depth environments. These data are summarized in table 1. Figure 6 plots evolutionary rates as measured by average species durations within each lineage

for each trophic strategy (triangles), with mean values graphed for each trophic group in the marine shelf zone (solid horizontal line), and for all groups regardless of habitat (dashed horizontal line) (data summarized in table 1).

These data show a strong relationship among bivalves between trophic strategy, resource stability, and evolutionary rates during the Cretaceous. Figure 6 and table 1, column 2a (marine shelf) show highest average species durations and slowest rates of evolution in species of *Nucula* (non-selective detritus feeders), somewhat shorter durations among selective detritus feeders and non-selective infaunal suspension feeders (not significantly different), about 30 % shorter durations for selective infaunal suspension feeders, and the most rapid evolutionary rates among selective epifaunal suspension feeders. An analysis of all lineages, exclusive of habitat (figure 6, dashed line; table 1, column 2b) does not clearly show this relation because rapidly evolving intertidal Donacidae lower the average duration for selective detritus feeders, and relatively more slowly evolving brackish water and freshwater bivalves raise the average species durations for both groups of selective suspension feeders. This points out the importance of testing for controls on evolutionary rate within single environmental régimes. In this more generalized analysis (figure 6, dashed line) the strong environmental overprint, diverse habitat characters, and variations in tolerance for environmental fluctuations among bivalves overwhelm the more sensitive relation between evolutionary rates, trophic strategy, and resource stability.

A less clearly defined relation between evolutionary rates and bivalve trophic strategy is shown in the analysis of species production rate (figures 3 and 5; table 1, columns 5 and 6). Table 1, column 6 is the most meaningful analysis: a measure of average species production rate over the entire time interval sampled. In this analysis, lineages of selective detritus feeders generate species at only half the rate of both selective and non-selective infaunal suspension feeders, and at only one quarter the rate of epifaunal suspension feeders. The data for non-selective detritus feeders (Nuculidae) show unexpectedly high rates of species production; this is attributed to the fact that, unlike other data, these represent an analysis of all species of *Nucula* rather than of individual lineages, which are difficult to define at present in this group. Undivided *Nucula* data would be expected to yield higher values in this type of analysis than averaged data from individual lineages.

Table 1, columns 3–5 analyse the magnitude of evolutionary events themselves, rather than rates of evolution. Among suspension feeding bivalves, the relation predicted by the theory is shown: non-selective suspension feeders show slightly lower peak speciation rates, and equivalent averaged rates during speciation episodes, compared with selective infaunal suspension feeders; both groups have values which are appreciably lower than those for epifaunal suspension feeders. But in all cases, detritus-feeding bivalves show remarkably high individual speciation peaks, numbers of speciation episodes, and speciation rates *during* peak radiations, which are equivalent to the highest speciation peaks obtained from suspension-feeding bivalves. The implications of this are interesting; detritus-feeding bivalves are longer-lived and have lower species production rates than suspension-feeding bivalves. However, when they do diversify, they undergo major evolutionary bursts at unusually high rates of species production. Both selective and non-selective detritus feeding Cretaceous bivalve groups show their highest radiation peaks at similar times, during the Middle Cenomanian transgression and during the Late Campanian–Early Maastrichtian regression (figure 3a, b). The protobranchs and tellinids may be responding to some major environmental (trophic?) crisis during these evolutionary

bursts, in which stress levels are severe enough to approach the tolerance limits of even these generalized benthonic groups. At present, the nature of this stress is unknown; it appears to be independent of transgressive–regressive history of the seaway. Cretaceous tellinids and proto-branchs may be reflecting an evolutionary pattern that is common among ecological generalists and eurytopes, reaching exaggerated speciation rates only during times of severe stress levels. Kauffman's observations (1970, 1972) that the most eurytopic epifaunal bivalves (Inoceramidae, Ostreidae) and ammonites (Scaphitidae) in the Cretaceous seaway of the Western Interior United States attained unusually high rates of evolution during late phases of epicontinental regression, representing maximum stress to marine environments, suggests that this hypothesis has some merit.

Evolutionary rates v. *habitat characteristics*

In marine habitats, diverse environmental factors may act to stress resident species populations: fluctuations in water chemistry, temperature, physical stress of wave, current and storm activity, and resources, competition for space and resources, predation, etc. These factors and stress levels diminish and become more predictable from shallow into deep water habitats, and from pelagic and epibenthic into deeper infaunal habitats at any depth. These stress gradients have fostered the hypothesis that evolutionary rates among similar organisms should diminish from shallow pelagic and epibenthic habitats into deeper water and infaunal habitats. Levinton (1973, 1974) demonstrated lower genetic variability and slower evolutionary rates among infaunal and deep water epifaunal bivalves than among epifaunal bivalves living at less than 300 m. Kauffman (1977a) demonstrated similar evolutionary patterns in lineages of Cretaceous Mollusca from the Western Interior United States. The hypothesis is tested further here, and restricted to suspension-feeding bivalves of Cretaceous normal marine environments to hold taxonomic and additional environmental factors as constant as possible. Data presented by Kauffman (1977a) are modified by the addition of new species data to lineages and slight revision of the radiometric time scale used to measure durations (Kauffman 1977b, 1978a).

A comparison of average species durations for lineages of marine suspension feeding bivalves (figure 7; table 1, column 2a) shows strong correlation between levels of habitat protection and evolutionary rate. Exposed, epifaunal lineages of shelf environments have the shortest *average* durations (1.25 Ma), and semi-infaunal bivalves the next shortest (1.8 Ma); predictably, the most exposed semi-infaunal taxa, like *Pinna*, have faster evolutionary rates than the barely exposed taxa, like *Idonearca*. Shallow infaunal taxa have even longer average species durations (2.04 Ma), moderately deep burrowing infaunal taxa the next longest durations (2.08 Ma), deep infaunal taxa the next (2.28 Ma), and finally deep water epifaunal taxa the longest average species durations (3.3 Ma) in this test.

A different measure of evolutionary rate, the average number of new species produced in the lineage per 10^6 years over the entire sampled interval (table 1, column 6; data from figures 3–5), shows the same general relation, with the notable exception of semi-infaunal bivalves; these show rates much lower than predicted by the hypothesis. Thus, shelf epifaunal bivalves produce, *on the average*, 1.6 species/Ma, semi-infaunal lineages 0.32 species/Ma, shallow and moderately deep burrowing bivalves 0.8 species/Ma, deep burrowing bivalves 0.17 species/Ma, and deep water epifaunal bivalves 0.36 species/Ma. The last are slightly higher than predicted.

The *magnitude* of evolutionary (speciation) events, rather than general rates of evolution, are shown in columns 3–5 of table 1. A broad but imperfect relation exists between 'magnitude'

and habitat. The highest speciation peaks among shelf epifaunal bivalves are, on the average, higher than those of semi-infaunal lineages, and these in turn higher than those of shallow infaunal taxa. Deep infaunal and deep water epifaunal taxa have even lower average speciation peaks. Moderately deep burrowing infaunal taxa show a reverse in this trend for unknown reasons (data in table 1, column 3). This general relation also exists in an analysis of numbers of speciation episodes for each lineage. Table 1, column 4, shows that epifaunal and semi-infaunal lineages, whose habitats represent broad exposure to unpredictable environmental perturbations, show more speciation episodes on the average than do more protected infaunal taxa. No more refined trends are shown by these data, or by calculations of the average number of species produced per speciation peak for diverse habitats (table 1, column 5).

In summary, both measures of evolutionary rates within lineages, but especially that based on average species duration, show a strong relationship between rate and habitat which reflects the degree to which a habitat protects resident organisms from unpredictable environmental perturbations and stress. Bivalves living in more exposed habitats have more numerous and higher average speciation peaks during their evolutionary history than do infaunal lineages.

Evolutionary rates v. environmental tolerance (eurytopy)

Two recent studies have suggested a direct relation between evolutionary rates and the degree of genetically controlled tolerance to environmental fluctuations (eurytopy v. stenotopy) in lineages. All other factors being equal, it is this factor which determines the degree to which populations are *biologically stressed* by unpredictable environmental perturbations. Thus, highly eurytopic taxa living in what has been termed 'high stress' physico-chemical environments (e.g. the intertidal zone) are not easily stressed *biologically* because they are adapted to predictable high level fluctuations in the natural environment. These taxa should theoretically evolve more slowly than taxa from less variable, more protected environments when subjected to equal environmental perturbations through time.

Jackson (1972, 1973) demonstrated this relation; he recorded slower rates of evolution, reflecting lower biological stress to populations and more effective dispersal potential, in species of Lucinidae, Veneridae, and Tellinidae living in tropical marine environments less than 1 m deep (a highly variable physico-chemical environment) than for more stenotopic counterpart species living in deeper shelf environments with lower *normal* levels of environmental fluctuation. Kauffman (1970, 1972) showed that, given a time–stress gradient associated with major marine regression in epicontinental seas, Cretaceous molluscs having stenotopic modern counterparts became stressed and showed peak rates of evolution and extinction early in regression (low-level physico-chemical changes); moderately eurytopic organisms peaked in mid-regression; and the most eurytopic lineages showed highest rates of evolution and major speciation peaks during latest regression, associated with the most severe physico-chemical 'stress'.

This hypothesis is further tested here by comparing evolutionary rates among Cretaceous bivalves from highly variable environments (intertidal, brackish, and freshwater fluvial habitats) with those in moderately variable habitats (shelf epifaunal, semi-infaunal, and shallow infaunal niches), and with those from slightly variable environments (deep water epifaunal and deeply buried infaunal shelf habitats). The data on lineages presented by Kauffman (1977a) are modified here by the addition of more species and revision of the radiometric time scale used to measure rates (Kauffman 1977b, 1978a).

Figure 7 and table 1, column 2a record evolutionary rates as measured by average species

duration within lineages for these various habitats. As predicted by the theory, bivalves from highly variable fluvial and slightly less variable estuarine brackish water environments show very long average species durations, and slow evolutionary rates. These groups today have remarkable abilities to cope with gross changes in turbidity, temperature, desiccation, salinity, etc. and, like Jackson's shallow subtidal bivalves (1972, 1973), are difficult to stress biologically and are conservative in their evolution. The single intertidal bivalve lineage tested (*Protodonax*) shows unpredictably short average species durations, but still slightly longer than those for shallow epifaunal marine bivalves, the most rapidly evolving group. Kauffman (1977a, p. 131) initially reported average species durations of 2.8 Ma for Cretaceous Donacidae from this region; data on additional species, and refinement of range data on others, has considerably lowered this figure to 1.3 Ma.

Thus, from fresh water to epifaunal marine shelf habitats, data on species durations support the hypothesis that genetically determined levels of environmental tolerance (highest in fresh and brackish water organisms, lower in offshore shelf, normal marine bivalves) are inversely proportional to evolutionary rates. However, this trend does not continue among normal marine infaunal and deep water epifaunal bivalves, theoretically more stenotopic and subject to higher stress associated with even small environmental perturbations. Instead, average species durations become longer in progressively more protected habitats, approaching levels of brackish water taxa in deep water epifaunal bivalves (figure 7). This marine gradient in evolutionary rates (figure 7) reflects stronger control on rates by habitat strategy and degree of protection from stress situations, than by levels of environmental tolerance. Dispersal characteristics represent another factor which may overprint the effect of environmental tolerance in diverse bivalves.

A similar trend is shown by data on species production during the span of each studied lineage (table 1, column 6). Fresh and brackish water bivalves have very low levels of production (0.37 and 0.17 species/Ma respectively); average rates of speciation are twice as high in intertidal bivalves (0.67 species/Ma), and more than five times as high (1.59 species/Ma) in marine shelf, epifaunal bivalves. Diminished rates in deep water epifauna and infaunal bivalves again reflects progressively greater habitat protection from perturbations.

Finally, the highest rates of speciation (peak values, averaged, table 1, column 3a) and average species production rates during speciation events (table 1, column 5) are among offshore, marine shelf, relatively stenotopic epifaunal bivalves; the lowest values are among environmentally tolerant intertidal, brackish, and freshwater bivalves. This agrees with Jackson's results comparing normal tropical marine shelf bivalves with counterparts living in less than 1 m of water (1972, 1973).

Evolutionary rates v. *eustatically generated variation in stress intensity*

In the Western Interior and Gulf Coastal Plain regions of North America, significant environmental changes in the Cretaceous marine ecosystem were predominantly related to a series of major eustatic and associated temperature–salinity fluctuations which produced alternating transgressions and regressions of shallow shelf and epicontinental seaways (figure 2). Changes of several hundred feet in sea level were involved, with strand migrations of hundreds of miles during each episode. In general, epicontinental transgressions were times of expanding, diversifying habitats, ameliorating climates, and generally low stress levels except for those generated by biological competition. Rapid evolutionary rates occurred only among taxa radiating into

new niches, pre-adapted to rapidly replace older taxa in occupied niches, or among taxa stressed through biological competition during early succession. Regression represented times of deteriorating marine environments, decreasing ecospace and niche diversity, higher variations in temperature, water chemistry and turbidity, and increased competition for space and resources. These conditions imposed higher levels of biological stress and more frequent environmental perturbations on the entire ecosystem, suggesting that these should have been times of more rapid evolution.

Kauffman (1970, 1972) tested numerous lineages of Cretaceous molluscs against this hypothesis, and found clearly defined relations between evolutionary rates and eustatic history. Most tested lineages showed little or no speciation during early to mid-transgression, and their highest rates of evolution, greatest and most numerous speciation events, and in some cases their greatest diversity during higher stress regression events, or associated with major changes in temperature and salinity near peak transgression. Lineages which showed major speciation peaks near peak transgression and early in regression were mainly offshore pelagic and benthonic stenotopes, as well as Tethyan migrants during peak transgression and severely stressed by lowering temperatures and salinities in the Western Interior basin during early regression (Kauffman & Scholle 1977). Moderately eurytopic taxa showed speciation peaks at mid-regression, and the most eurytopic taxa and moderately stenotopic nearshore (sand facies) taxa showed speciation peaks late in regression. These data suggest a relation between degree of eurytopy and stress intensity over a time–stress gradient (Kauffman 1970, 1972).

This relation can be further tested with the data generated in the present study. Figures 3–5 outline transgressive (T)–regressive (R) history of North American seaways at the top, using the system of Kauffman (1977b), against which the occurrence and magnitude of speciation peaks have been plotted for diverse bivalves. Many more bivalve lineages, representing a much greater diversity of habitats and ecological strategies, are used here than in previous tests. These data are summarized in table 1, column 7.

Figures 3–5 show that the highest speciation peaks for each lineage predominantly occur during regressive pulses; 57 % of the peak speciation events for each lineage are during regression; 17 % are equal between transgressive and regressive peaks, and only 26 % occur during transgressive episodes. These analyses include lineages like *Thyasira* and *Nymphalucina* whose prime habitats and thus principal radiations develop mainly during transgressions. Without these explanable exceptions, the predominance of major speciation events during regressive pulses is even stronger. Of all the ecological groups (trophic, habitat, etc.) tested, only 2 show a predominance of speciation events during transgression: non-selective, suspension feeding infaunal bivalves (mainly *Thyasira*; see explanation above), with 10 transgressive speciation events to 1 during regression, and the shallow water epifaunal suspension feeders (25 speciation events on transgressive pulses, 20 during regression). All other groups have speciation episodes predominantly associated with regressive pulses. High levels of radiation among epifaunal benthonic shelf bivalves during transgression may relate to the fact that they inhabited the suite of environments that showed the greatest diversification during transgression, with many new niche opportunities.

Overall, these analyses support the contention that the greatest amounts and the highest rates of speciation among Cretaceous Bivalvia took place during regressive, high stress episodes in shelf and epicontinental seas. Major exceptions can largely be explained by the fact that their habitats were mainly developed, occupied, and ultimately stressed during transgressive

and earliest regressive history. Although comparison of the total number of speciation peaks sampled in this study shows only a slight edge in regressive speciation episodes over those occurring in transgression (109 and 104, respectively), removal of data for those groups whose preferred habitats develop mainly as transgressive phenomena yields 79 (57 %) regressive speciation episodes, and 59 (43 %) transgressive episodes for the rest of the lineages (table 1).

Of particular interest in the analysis of fresh water Bivalvia (figure 4a; table 1, column 7) is that all genera have their highest speciation peaks, and collectively freshwater bivalves have relatively more speciation peaks, during regression of marine epicontinental seaways from the Western Interior United States and southern Canada, as predicted by Hanley, Kauffman & Russell (1978). The prime habitants for these groups, associated with wet lowlands common to broad coastal plains, were most extensively developed during marine regression; logically, this would also have been the time when opportunities for radiation of freshwater taxa was greatest.

Conclusions

Data on evolutionary rates and patterns are now available for more than 50 lineages of Cretaceous Bivalvia from the Western Interior and Coastal Plain regions of North America. These lineages represent diverse habitat strategies – from freshwater to deep marine, and from epifaunal to deep burrowing infaunal niches – which characterize the normal range of environments inhabited by modern bivalves. They also represent all major trophic strategies among bivalves except microcarnivores, and a broad range of morphologic complexity. These data thus provide a basis for testing various hypotheses concerning evolutionary rates among Metazoa, including especially tests of evolutionary rates v. morphological complexity (? reflecting genetic complexity), v. habitat characteristics, v. trophic strategy and resource prediction, v. environmental tolerance, and rates v. stress intensity. Comprehension of these relations, and determination of the degree to which evolutionary rates and patterns are predictable, greatly enhance studies in bivalve phylogeny and classification. Determination of evolutionary rates with the use of a detailed radiometric time scale based mainly on K–Ar analyses of volcanic ashes and bentonites allows, for the first time, objective interpretation of the tempo of evolution among bivalves and other invertebrates, and meaningful comparisons with vertebrate evolution. The principal results of this study are as follows:

(1) Evolutionary rates vary greatly within single lineages subjected to broad fluctuations in the environment through geological time. Rates also very between bivalve lineages, representing different ecological strategies, that cohabit any area and are thus broadly subjected to the same major changes in environment through time. There is *no* constant rate of evolution, no matter how it is measured, for any lineage or for the class as a whole.

(2) Measured radiometrically, evolutionary rates among bivalves tested in this study range from very slow, with individual species durations as long as 18 Ma (among *Nucula*) and averaging as high as 5.63 Ma/species among tested freshwater lineages, to rates that are very rapid and comparable to those recorded for much more complex Cainozoic mammals. The average species duration of shelf dwelling, selective suspension-feeding, epibenthic bivalves from the Cretaceous is 1.25 Ma; the average species production rate for all sampled lineages is 1.59 species/Ma. Within this group, certain lineages of Inoceramidae and Ostreidae have average durations of 0.19, 0.17, 0.08, and 0.06 Ma during parts of their evolutionary history with species generation rates reaching a peak of 9 species/Ma in *Mytiloides* and 7 species/Ma within

Inoceramus (*Inoceramus*) (figure 5*c*). Taxonomic units used in this study are those of varied workers in these analyses and do not reflect a single philosophy.

(3) Evolutionary patterns range from gradualistic to strongly punctuated or stepwise among Cretaceous Bivalvia, even within single lineages. In general, punctuated patterns are most commonly associated with evolution during high stress situations, and/or with rapid onset of stress conditions. More gradualistic patterns are characteristic of ameliorating or low stress environments. The data further suggest that more gradualistic patterns, represented by low numbers of small scale speciation peaks, are most characteristic of eurytopic taxa and ecological or trophic generalists; irregular, punctuated evolutionary patterns with scattered, high-level bursts of speciation separated by periods of low species production are more characteristic of stenotopic, ecological specialists among bivalves. But even eurytopic trophic and habitat generalists show rare but prolific evolutionary bursts, and these may be very much out of proportion to the normal speciation patterns.

(4) Various tests for evolutionary rates *v.* morphologic complexity among studied Cretaceous bivalve lineages show *no* well defined correlation. In all but one test, simple to moderately complex bivalves showed equivalent or faster evolutionary rates than the morphologically more complex taxa. From this it is implied that genetic complexity, to the degree that it can be determined from morphological complexity of shell characters, does not play a dominant rôle in determining evolutionary rates. Certainly the number and diversity of bivalve shell characters for any lineage does not relate to measured evolutionary rates.

(5) There exist very strong relationships between evolutionary rates, trophic strategy, and stability of trophic resources. Trophic generalists evolve more slowly than trophic specialists because of greater stability in food resources. More specifically, tests on Cretaceous lineages indicate that there is a graded series of increasing rates of evolution (and decreasing average species duration) from non-selective detritus (deposit) feeders, to selective detritus feeders, to non-selective suspension (filter) feeders, to infaunal selective suspension feeders, to epifaunal selective suspension feeders. The last have the most sophisticated particle sorting and transport mechanisms. All data analysed in this test are from taxa inhabiting normal marine, shelf-depth environments.

(6) There exists a strong relationship between habitat characteristics and evolutionary rates among marine bivalves within the same trophic strategy (selective suspension feeders in the test case). Decreasing rates of evolution are recorded through a graded series of habitats ranging from shelf epifaunal bivalves (fastest rates), to semi-infaunal bivalves, to shallow infaunal forms, to moderately deep burrowing forms, to deeply burrowed taxa, and finally to deep water epifaunal bivalves (slowest rates). Decreasing evolutionary rates in this analysis are inversely related to increasing degree of habitat protection from unpredictable environmental perturbations, or stress levels. Of all tests conducted in this study, the relation between evolutionary rates and habitat strategy seems to be the strongest, and predominates over other relations (e.g. *v.* trophic strategy, etc.) in situations where multiple factors act in concert to affect evolutionary rates.

(7) In a test of environmental tolerance (stenotopy *v.* eurytopy) as a factor influencing evolutionary rates, a direct relation was found between the range of predictable environmental fluctuations to which an organism is adapted and its evolutionary history. The most slowly evolving taxa are those which exclusively occupied highly variable habitats (e.g. freshwater, brackish water); intertidal bivalves have, surprisingly, higher evolutionary rates, but still

slower than those of fully marine forms. Epifaunal marine bivalves from offshore, shelf-depth environments have the fastest rates determined. Among lineages used in this analysis, they occupied some of the least variable environments, but which today are also those most commonly affected by unpredictable environmental perturbations.

(8) A strong relationship exists between evolutionary rates, degree of eurytopy, and levels of stress in changing global environments. Rates of onset of stress conditions also exercise an important control on rates of evolution. Ameliorating, low stress environments associated with marine transgression generally foster low rates of evolution except among: (a) lineages that are highly stressed through biological competition (succession) early in transgression; (b) lineages that are preadapted to a newly developed, unoccupied niche, or better adapted to a poorly occupied niche, and which undergo rapid radiation during low stress, marine transgressive phases; or (c) lineages whose preferred habitat develops and spreads primarily or exclusively during periods of climatic amelioration.

Even including these exceptions, most speciation events within Cretaceous bivalve lineages, and the highest rates of evolution at the species level, take place during environmental decline and increasing stress factors – physical, chemical, and biological changes associated with marine regression. During environmental decline, more stenotopic taxa generally attain their peak evolutionary rates, and subsequently highest levels of extinction, during early stages of regression and low physico-chemical stress levels; moderately stenotopic or moderately eurytopic taxa peak midway through major periods of environmental decline; and eurytopic taxa exhibit their highest rates of speciation and extinction during later phases of environmental decline associated with high stress levels. Rates of environmental decline generally determine rates of speciation and extinction, and spacing of these events during each of these phases.

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