

## The shape of evolution: a comparison of real and random clades

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*Abstract.*—The history of life is replete with apparent order. Much of this order may reflect the deterministic causes conventionally invoked, but we cannot be sure until we measure and subtract the order that arises in simple random systems. Consequently, we have constructed a random model that builds evolutionary trees by allowing lineages to branch and become extinct at equal probabilities. We proceed by dividing our simulated tree into clades and by comparing their sizes and shapes with the patterns exhibited by “real” clades as recorded by fossils.

We regard the similarity of real and random clades as the outstanding result of this comparison. In both real and random systems, extinct clades arising after an “ecological barrel” had been filled have their maximum diversity at the midpoint of their duration; clades arising during the initial “filling” reach an earlier climax during this preequilibrium period of rapid diversification. However, some potential differences also emerge. Clades still living are much larger than extinct clades. We may attribute this to the morphological superiority of survivors, but we can also simulate it in a model that chooses the originators of clades at random. Real clades undergo greater fluctuations in diversity than do random clades, but the effect is not marked.

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### Purpose and Procedure

Does the history of life have a characteristic “shape”? The illustrations conventionally used by paleontologists to depict the diversity of life through time have an undeniable morphology (Figure 1), and paleontologists have spent a century trying to interpret the evident order of these diagrams. Why, for example, do so many clades wax and wane simultaneously? Why do some pairs fit like a jigsaw puzzle? Clams wax while brachiopods wane; teleost fishes wax while ammonites wane. Does this coupling between groups with similar ecological roles signify the competitive replacement of less efficient by more advanced forms?

Philosophical determinism has been the guiding idea behind conventional interpretations. The apparently ordered pattern of clade diversity diagrams has been universally taken as sufficient reason for assuming defi-

nite causes related specifically to the unique nature of different organisms and times. But we know that purely stochastic systems can generate high degrees of apparent order (5 heads in a row about 1 time in 32 trials—and if the history of life provides anything, it provides many trials). Moreover, because evolution is so largely Markovian (next state dependent, in part, upon the last), the probability of apparent order is much higher than in such “independent events” processes as coin tossing. We have therefore constructed a stochastic model for the generation of clade diversity diagrams (Raup et al. 1973). We do this not because we believe that life’s history is ontologically random—though it might well be in several important respects—but rather because we regard it as the best approach for inferring cause in the study of clade diversity diagrams (for a similar approach with different

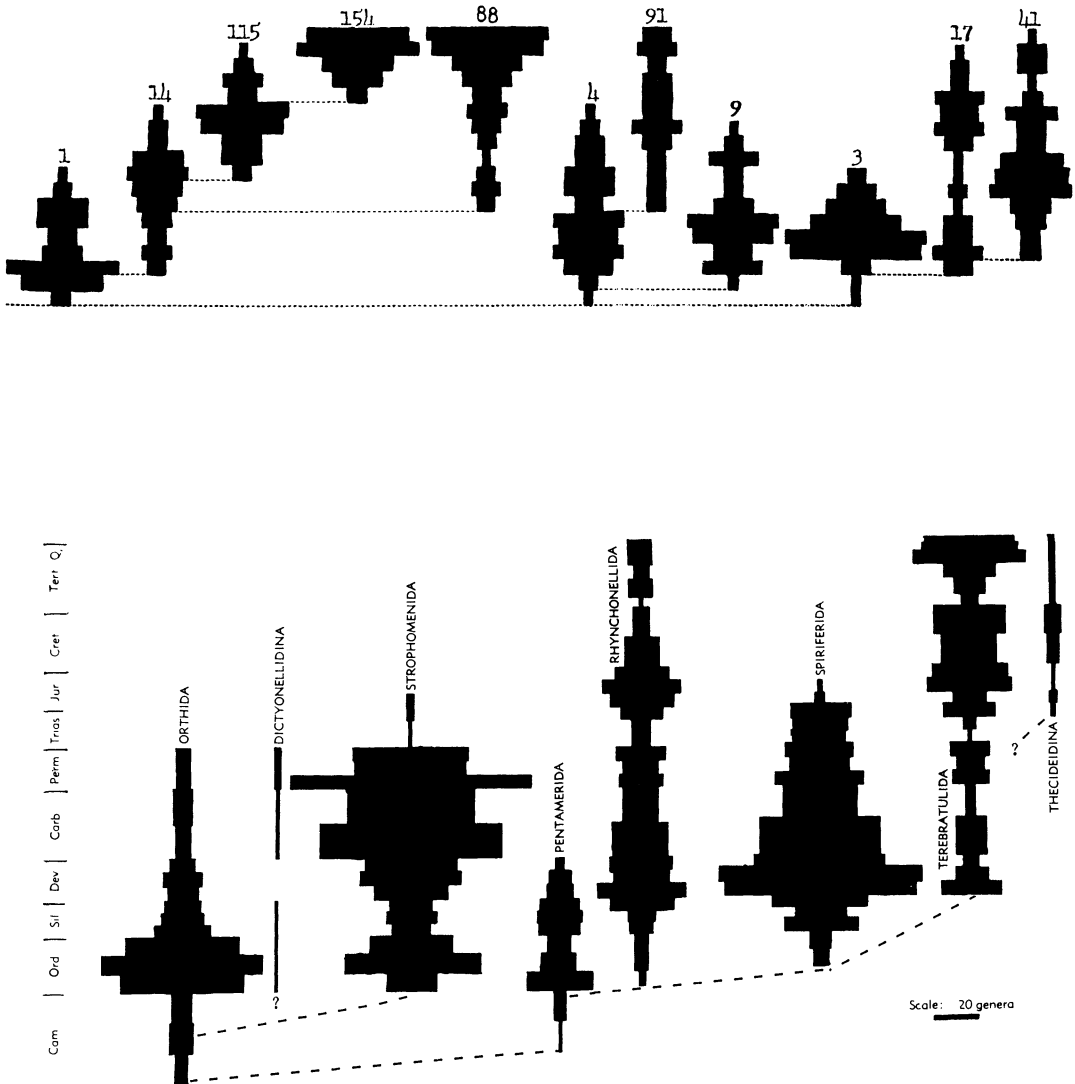


FIGURE 1. Comparison of random with real clades. Top: clades for one run of the MBL program at branching and extinction probabilities of 0.1. Bottom: real clades for genera within orders of brachiopods, from *Treatise on Invertebrate Paleontology*.

conclusions, see Van Valen 1973). Until we know what degree of apparent order can arise within random systems, we have no basis for asserting that any pattern in the history of life implies a conventional cause for its generation. We use our stochastic system as a "base level model" or "criterion of subtraction" for ascertaining what amount of apparent order requires no deterministic cause. We may then seek standard explanations for the residuum of order. Despite a century of activity, the study of clade diversity diagrams

has never risen above the level of description, despite some very ambitious attempts in the inductive tradition (Müller 1961, 1974). We suggest that any explanatory role will require a criterion for the partitioning of overt order into potentially random and non-random components.

We confess to a larger, ulterior motive in this and related studies (Raup and Gould 1974; Schopf et al. 1975). We believe that paleontology—the most inductive and historical of sciences—might profit by applying

some deductive methods commonly used in the non-historical sciences (without sacrificing its important documentary role for the history of life). We may seek an abstract, timeless generality behind the manifest and undeniable uniqueness of life and its history. We take as our guide the recent success of simple, general models in the other branch of natural history most celebrated for the complexity and uniqueness of its subject—ecology (MacArthur and Wilson 1967; Levins, 1968; May 1973). Consequently, we have developed “untimebounded” and “untaxonbounded” models for the simulation of patterns in form and diversity during the history of life—i.e., our models treat all times and taxa alike.

In this study, we proceed in the following way:

1. We generate clade diversity diagrams with our stochastic model.

2. We devise a set of “clade statistics” to measure the size and shape of these diagrams.

3. We determine the frequency distributions of these clade statistics for stochastic clades generated over a wide range of probabilities for branching and extinction of lineages. (This range almost surely includes all reasonable values for actual lineages.)

4. We compute the clade statistics for real clades at several taxonomic levels (orders within classes for all life, families within orders, and genera within families).

5. We search for features of real clades that cannot be simulated in any reasonable way within our stochastic system. We deal here only with the size and shape of clades, not their stratigraphic positions. Thus, we do not treat such clearly non-random events as the Permian mass extinction (the simultaneous waning of most clades) unless their effects are recorded in the shapes of clades (if, for example, clades wiped out in mass extinctions have terminal shapes statistically different from clades that became extinct in more “normal” times).

## The Model

Our simulations begin with a single lineage at time 1 and run for as many intervals as we specify (see Raup et al. 1973 for details of procedure). In each interval, automatically generated random numbers determine the

fate of each lineage. With predetermined probabilities lineages may (i) become extinct, (ii) branch to yield two lineages at the next interval, or (iii) persist without branching to the next interval. We make the probabilities of extinction and branching equal. The same probabilities apply to all lineages in all intervals—the model is “untaxonbounded.” The MBL program has several options, all incorporating this basic stochastic feature. (The MBL program, named for the Marine Biological Laboratory at Woods Hole where we met several times to plan our joint work, contains many options suiting it for use as a general-purpose “evolution machine.” Inquiries should be directed to D. M. Raup at the University of Rochester).

We consider two options for comparison with real clades in this work:

- (i) A damped-equilibrium (DE): In analogy with the equilibrium models of theoretical population ecology, we specify an “optimum” number of coexisting lineages for any interval (this optimum number applies to all intervals in our “untimebounded” model). Stochastic departures from this optimum are damped by raising the probability of extinction when it is exceeded, and augmenting the probability of branching when an interval contains “too few” lineages. This option also introduces a preequilibrium phase into our otherwise untimebounded system. Since we begin with a single lineage, our damping function assures that branching probabilities will exceed extinction probabilities for the first few intervals until the optimum is reached (Never more than 5–10% of all intervals). The actual history of life included a preequilibrium phase of rapidly rising diversity; it is called the Cambrian “explosion.”

- (ii) Freely floating (FF): No optima, no damping and no preequilibrium phase at the beginning of the run. We begin with a single lineage. Branching and extinction probabilities are equal and unchanging throughout the simulation. Of course, many trials abort by early extinction of all lineages. Other runs never generate a tree of any appreciable diversity. Still others “explode.”

The result of these procedures is an evolutionary tree containing hundreds of lineages. But paleontologists rarely study patterns of

diversity by considering the fates of individual lineages; we map the temporal distribution of coherent larger groups (reptiles or brachiopods, for example)—i.e., we consider major limbs of the evolutionary tree, or clades. In the absence of morphology, we follow a procedure for defining clades that conforms to biological rules and basic criteria of judgment in taxonomy:

(i) Clades must be monophyletic.

(ii) Clades must have a minimum size (one lineage persisting for one unit contributes 1 to the size of a clade. A clade of size 100 may, for example, contain 10 lineages each persisting for 10 intervals, or a single lineage surviving for 100 intervals). Since a clade cannot contain monophyletic subclades that reach minimum size, this rule also places a statistical upper limit on the size of a clade. If these rules permit more than one partitioning of the tree into clades (this happens rarely), we give preference to clades with earlier origins in time.

Each run of the simulation program provides a set of clade diversity diagrams (Figure 1). These sets provide the basic data for our statistical analysis of size and shape in stochastic clades.

### Clade Statistics

The questions asked by paleontologists about the morphology of clade diversity diagrams can be reduced to a few general and obvious concerns: How big is a clade (temporal duration and number of members at any one time)? How wide is it (diversity within intervals compared with temporal duration)? How much does its diversity fluctuate through time (fairly constant or varying greatly with alternating periods of luxuriant branching and near extinction)? Where is it widest (are groups more diverse near their origin, their endpoints, or near the middle of their total "life span"?). Important questions about the history of life depend upon this information. If, for example, clades are characteristically widest near their bottoms, we might claim that they generally undergo an early period of vigorous adaptive radiation following the invasion of new and unexploited environments; later history would be dominated by a slow weeding out of less adapted forms. But if clades are widest near their

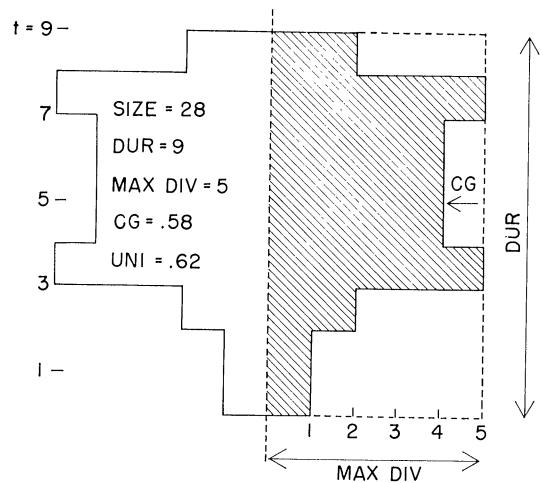


FIGURE 2. Clade statistics used in this analysis. DUR = duration; MAX DIV = maximum diversity; CG = center of gravity; UNI = uniformity; see text for definitions.

tops, we might argue that steadily increasing diversity marks the history of clades in "normal" times, while rare episodes of mass extinction regulate life by acting as *dei ex machinis* to cut off groups at the height of their success. And if clades are generally widest near their midpoints, perhaps they merely follow a stochastic pattern set by their definition of a single origin and a minimum size—lineages that leave enough descendants to form a clade drift to their maximum diversity and eventually peter out.

We therefore invented the following measures to capture this basic information as best we could (Figure 2):

1. **SIZE.** A combined measure of persistence and diversity (each lineage contributes one unit of clade size for each interval of time in which it lives).

2. **Duration (DUR).** The number of time intervals through which a clade survives (with no reference to its diversity within these intervals).

3. **Maximum Diversity (MAX DIV).** The number of lineages living in the time interval during which the clade is widest.

4. **Center of Gravity (CG).** A measure of the relative position in time of the mean diversity. We scale duration from zero (time of origin) to one (time of extinction), and measure the position of the mean on this scale. Clades that are most diverse below

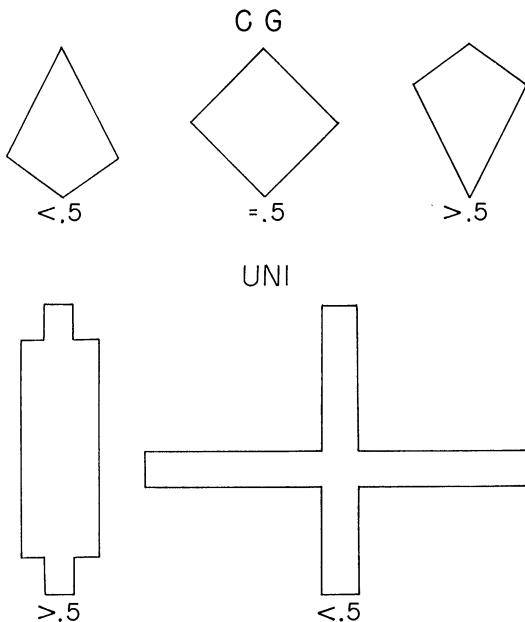


FIGURE 3. Shapes of clades that yield high and low values of CG (center of gravity) and UNI (uniformity).

their midpoints have centers of gravity less than 0.5, while clades that enjoy their greatest success past the midpoint of their existence have CG's greater than 0.5 (Figure 3).

5. Extent of fluctuation in diversity (UNI, for uniformity). We simply circumscribe a rectangle about the clade dimensions of MAX DIV and DUR and calculate the percentage of the rectangle's area occupied by the clade (Figure 2). Parallel sided clades with no variation in diversity fill their rectangles completely (UNI = 1). Clades of modest diversity except for a few periods of very high diversity have low values of UNI (Figure 3). Diamonds (clades which begin and end with single lineages and have their maximum diversity at their midpoints) have UNI's of 0.5. We are well aware that information theory provides more "sophisticated" measures of "information" and "evenness" to capture this property of fluctuation (see, e.g., Wilson and Bossert, 1971), but we prefer our simple-minded and easily visualized, geometric assessment. We computed information and evenness for all clades and gained no insight not provided by our measure of UNI. These measures are, moreover, largely redundant with UNI. The average correlation coefficient

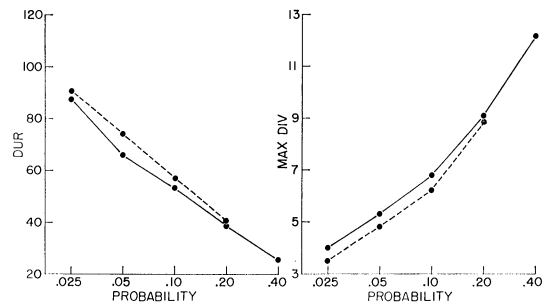


FIGURE 4. The distribution of mean values for DUR (duration) and MAX DIV (maximum diversity) for different probabilities of branching and extinction in the stochastic simulations. Solid line: damped equilibrium model. Dashed line: freely floating model.

$r$  of UNI and evenness is 0.88 for clades of families within orders in seven groups.

### Distribution of Clade Statistics in Simulations

When we alter systematically the probability for branching and extinction of lineages in the stochastic simulation, these clade statistics behave in a consistent, well-graded and predictable manner. We take this as an indication that our invented measures are successfully reflecting some major properties of our system. Consider, for example, the three measures of magnitude: size, maximum diversity, and duration: for either the damped equilibrium or freely floating model (Figure 4 and Table 1), clades are longer (high DUR) at low probabilities of branching and extinction and less persistent in time at high probabilities. Maximum diversity follows an opposite pattern (Figure 4); it increases as the probability for branching and extinction rises. Thus, clades are long and skinny (i.e., never very diverse, but stubbornly persistent in time) at low probabilities, and short and fat at high probabilities (highly successful for a time, but doomed to a short life). Size itself decreases slightly with rising probabilities. Clades are defined by a rule of minimum size. At high probabilities, with copious branching, clades can be selected near this minimum since so many possibilities for subdivision exist. However, at low probabilities with limited branching of new lineages, large and discrete clades can greatly exceed the mini-

TABLE 1. Mean values for clade statistics in stochastic systems. 1. DE = damped equilibrium model; FF = freely floating model. DE means are based on 5 runs; FF means on 10 runs. Size of total sample (for SIZE, MAX DIV, and DUR): DE model—90 at .025, 99 at .05, 103 at .10, 106 at .20, and 85 at .40. FF model—20 at .025, 30 at .05, 57 at .10, and 100 at .20. Size of extinct sample (for CG and UNI): DE model—31 at .025, 56 at .05, 74 at .10, 81 at .20, and 70 at .40. FF model—5 at .025, 11 at .05, 37 at .10, and 78 at .20. The MBL program is very difficult to run in the FF mode at  $p = .40$  since runs almost always abort by random extinction of all lineages during the first few intervals when the tree is very small.

| Probability of branching and extinction | .025  | .05   | .10   | .20   | .40   |
|---|-------|-------|-------|-------|-------|
| DUR (DE) <sup>1</sup>                   | 87.6  | 65.8  | 53.1  | 38.8  | 25.8  |
| DUR (FF)                                | 90.8  | 74.0  | 56.2  | 40.5  | —     |
| MAX DIV (DE)                            | 4.0   | 5.3   | 6.8   | 9.1   | 12.2  |
| MAX DIV (FF)                            | 3.5   | 4.8   | 6.2   | 8.9   | —     |
| SIZE (DE)                               | 176.8 | 161.7 | 155.2 | 146.6 | 138.2 |
| SIZE (FF)                               | 151.9 | 159.1 | 153.9 | 150.8 | —     |
| CG (DE)                                 | .457  | .475  | .488  | .505  | .542  |
| CG (FF)                                 | .501  | .517  | .500  | .517  | —     |
| UNI (DE)                                | .552  | .496  | .473  | .440  | .462  |
| UNI (FF)                                | .625  | .496  | .461  | .444  | —     |

mum without “evolving” any descendant clades.

For the dimensionless measures of clade shape, UNI and CG, we focused on extinct clades only. Clades still extant at termination of the program have yet to run their course; many of their measures are strongly influenced by this artificial truncation. Average CG, for example, is always higher in extant than in extinct clades (both in the real world and in the simulations). Many extant clades are artificially terminated at or near the height of their success; these downwardly pointing triangles have very high values of CG.

The idealized equilibrium diamond has a CG of 0.5 (widest at the midpoint of its duration). The distribution of CG in the damped-equilibrium model displays two features that depart from this expectation (Figure 5): 1) mean CG rises steadily with increasing probabilities of branching and extinction; 2) at low probabilities, mean CG dips below 0.5 (solid line of Figure 5). The steady rise is a consequence of our definitions. Our clades are constrained, by the rule of monophyly, to begin as single lineages—i.e., they must have

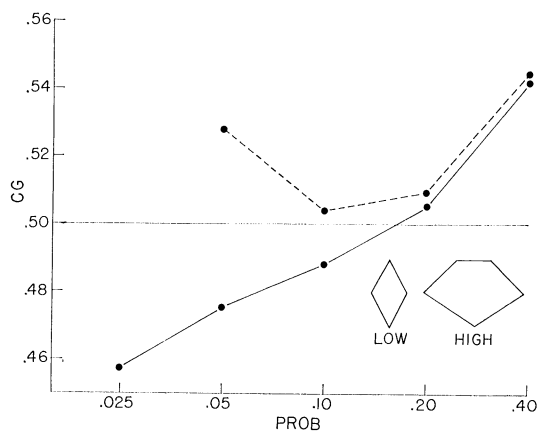


FIGURE 5. Distribution of mean values for CG (center of gravity) at different probabilities of branching and extinction in the stochastic simulations. Solid line: damped equilibrium model for all extinct clades. Dashed line: damped equilibrium model for clades arising after the initial preequilibrium phase. The inset shows average clades for low and high probabilities (abscissal values).

a diversity of 1 during their first interval. However, they may end by the simultaneous extinction of several lineages—i.e., they may have truncated tops, though they must have pointed bottoms. Clades with pointed bottoms and truncated tops have CG's in excess of 0.5 (Figure 5), and the more pronounced the truncation, the higher the CG. At low probabilities for branching and extinction, the chance that a clade will be extirpated by simultaneous extinction of several lineages becomes very small. Clades are “pointed” at both their bottoms and tops, and CG nears 0.5. At higher and higher probabilities, CG rises as the chance of simultaneous wipe-out steadily increases.

We can explain the rise in CG, but how can its value ever get below 0.5? The answer is that it can't in a truly untimebounded system. But our DE model contains a preequilibrium phase. Our damping function causes branching rates to exceed extinction rates early in our simulation when diversity is rising from a single initial lineage to its equilibrium value. Many extinct clades originated during this preequilibrium part of the simulation—i.e., they passed their early life in this period of high origination and low extinction, and their declining days during equilibrium constancy. Thus, they expanded rapidly dur-

ing their early history, and petered out slowly later on. This gives them a fat bottom, an attenuated top and a CG well below 0.5. At high probabilities, this effect is swamped by rising chances of upper truncation, and mean CG stays above 0.5. We are confident that the preequilibrium phase alone produces mean values below 0.5, and that mean CG will be at or above 0.5 in a truly untime-bounded, stochastic system for two reasons: i) If we consider only those extinct clades arising *after* the preequilibrium phase (dotted line of Figure 5), then mean CG remains above 0.5 at all probabilities. ii) In the FF model with no preequilibrium phase (Table 1), mean CG for extinct clades never drops below 0.5.

Figure 6 and Table 1 show the distribution of UNI for extinct clades in both the DE and FF models. UNI is high at very low probabilities of branching and extinction. With so little opportunity for branching and extinction, we begin to get parallel-sided clades consisting mostly, if not entirely, of single lineages that survive the entire simulation without producing descendants or succumbing themselves. These clades, with their UNI of (or near) 1.00, raise the mean value sharply. At all higher probabilities, UNI is slightly, but consistently, lower than 0.5. A perfect diamond, our idealized model of an equilibrium clade, has  $UNI = 0.5$ ; why, then, is mean UNI lower in our simulations? UNI is highly sensitive to slight changes in maximum diversity because width of the circumscribed rectangle is set by the greatest number of coexisting lineages. If one time interval has an unusually large number of lineages, the circumscribed rectangle will be large, and UNI of the enclosed clade consequently low (Figure 3). The stochastic features of our model seem to guarantee that some simulated clades—enough to drive mean UNI below 0.5—contain an unusually large number of lineages at their maximum diversity.

### The Clades of Life

The idea of perfectly objective observation is always a myth, but the problem of bias is particularly acute in our situation. We wish to specify the size and shape of life's "real" clades, but we can only tabulate these

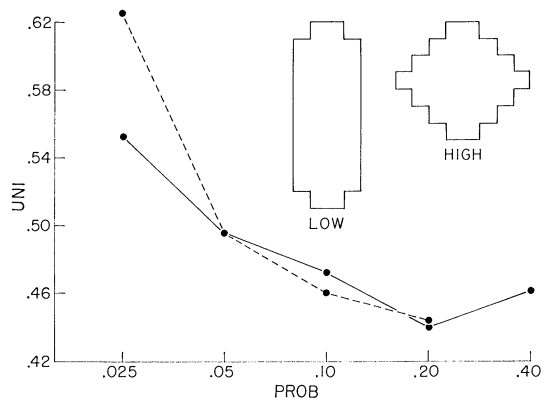


FIGURE 6. Distribution of mean values for UNI (uniformity) at different probabilities of branching and extinction in the stochastic simulations. Solid line: damped equilibrium model. Dashed line: freely floating model. The inset shows average clades for low and high probabilities (abscissal values).

clades through two stringent filters: the varying practices of taxonomists and the legendary imperfections of the geological record (Raup 1972). By "real" we only mean "based on the data of fossils as we best know them." We are as acutely aware as anyone of the great imperfection of the fossil record and of the arbitrary decisions and disparity of methods among taxonomists. The clade statistics reflect the true history of groups only through these filters. Clades of genera within families for Mesozoic ammonites, for example, are extremely short and fat. We do not deny that evolution may have been very rapid within this group, but prodigious oversplitting inspired by stratigraphic utility may be the primary cause of these unusual shapes. Likewise, the discovery of a single Recent monoplacophoran converted a short and relatively fat clade (ending in the Devonian) into a long attenuated clade persisting to the present day. The virtual absence of extensively fossiliferous deep-water strata in the fossil record assured this gap until a modern deep-sea dredge recovered a living form (shallow water monoplacophorans became extinct in the Devonian). We can rarely make a quantitative estimate of these biases—though one of us (DMR) is now engaged in just such an attempt. But we can usually be confident of their direction. Fortunately, in several crucial cases, these artificial biases work against a hypothesis we are trying to prove. If the

hypothesis is affirmed nonetheless, we may be fairly confident of its status.

We tabulated all real clades for which we could find sufficient data at three different ranks of the taxonomic hierarchy: orders within classes, families within orders, and genera within families. In each case, we treated the lower level as lineages forming clades at the next higher level. Genera within families represent the lowest practical level—the closest possible approach to true lineages (i.e., evolving species). Species level taxonomy in the fossil record is largely untabulated and highly variable in concept and application. We used the 77 stratigraphic intervals recognized in Harland et al.'s (1967) tabulation, *The Fossil Record*, (they actually use 74, but we broke their long Lower Cambrian series into the four stages recognized in the USSR). [To split the Lower Cambrian into four stages at both the ordinal and familial levels, we used Hupé (1960), Lochman-Balk and Wilson (1958), Palmer (1968), Rozanov (1967), Samsonowicz (1956), and Zhuravleva (1970)]. Late Precambrian (Vendian) metazoan identifications follow Glaesner (1971). We computed the age of each interval, using the absolute time scale in Harland, Smith and Wilcock (1964). Thus, clade statistics are not calculated by treating each interval as a unit duration; rather, we used Harland et al.'s (1964) estimates of absolute age, and scaled our measures accordingly. A lineage contributes one unit to the size of its clade for each million years that it lives. The range and sources of our data include:

1. Orders within classes. All of life, monerans to mammals to dicots—144 clades. Basic data on metazoa from Kukulova-Peck (1973), supplemented by the following: Archaeocyathids—from *Treatise on Invertebrate Paleontology* (E, revised). Coelenterates—supplemented with *Treatise* (F). Molluscan problematica—supplemented with *Treatise* (W). “Lower” invertebrates (“worms”)—supplemented with *Treatise* (W). Trilobitoidea—from *Treatise* (O). “Fishes”—from Harland et al. (1967). Algae—follows classification of Papenfuss (1955, p. 115). Range data for algae compiled from Harland et al. (1967), Orlov (1972), P. Embérger, (1968), A. R. Loeblich III (personal communication). Higher

plants—compiled from Harland et al. (1967), supplemented with the taxonomy of R. E. Scagel (1965).

2. Families within orders. There are 206 clades (birds, fishes, graptolites, echinoderms, bryozoans, coelenterates, archaeocyathids, brachiopods, and trilobites). These include all groups tabulated at this level in Harland et al. (1967), supplemented by the following: For echinoderms—*Treatise on Invertebrate Paleontology* (S, U); crinoids from Piveteau (1953); bryozoans—supplemented with *Treatise* (G); coelenterates—*Treatise* (F); Archaeocyathids—*Treatise* (E, v. 1, revised); brachiopods—*Treatise* (H).

3. Genera within families. For all major groups recorded with adequate stratigraphic control in the *Treatise on Invertebrate Paleontology* (Moore 1955–1976), plus mammals from Simpson's (1945) classification—1442 clades (graptolites, corals, bivalves, archaeogastropods, cystoids, ostracodes, ammonoids, trilobites, echinoids, nautiloids, brachiopods, and mammals). (A few important treatise volumes have not yet been published, crinoids and higher gastropods in particular. Some early volumes do not provide adequate stratigraphic resolution for genera—bryozoans, for example.)

In addition, we calculated clade statistics for one set of data on lineages separated by several taxonomic levels from their clades—genera within classes or phyla, as recorded in Müller (1961). All statistics were calculated by PANORAMA, a FORTRAN program written by J. J. Sepkoski. PANORAMA draws clades, tabulates diversity in each interval, plots total diversity against time, prints statistics for each clade, and calculates means and variances for all clade statistics in the total sample (with Holocene records included or excluded for extant clades), and for extinct and extant clades separately.

## Differences Among Real Clades

The quantification of real clades permits two different kinds of inquiry—comparisons among real clades, and the contrast of real and random clades. Potential differences between real and random clades form the subject of this paper, but we wish to emphasize the possibilities offered by our techniques



for comparison among real clades. We envision two major paths of inquiry:

1. Differences among groups at a taxonomic level.

Table 2 presents clade statistics for all groups considered at our three taxonomic levels. Differences within a level are often striking. For our most important tabulation of genera within families, extinct mammal and ammonoid clades stand apart from all other groups in their small sizes (the only two groups with mean size less than 100). Extinct coral clades, on the other hand, are larger than all others and more diverse at their maxima (highest MAX DIV). But we can interpret these differences as reflecting either real variation in evolutionary pattern or artificial distinctions of taxonomic practice—and we do not know how to distinguish between these alternatives. We might argue that ammonoids and mammals, as “advanced” animals, evolve very rapidly and easily develop new morphologies that demand recognition as families; clades for families are therefore short (DUR) and small. Corals, as simple and “primitive” creatures, rarely evolve new features that warrant the award of familial status; hence, their clades are large and diverse. But the differences might be purely artificial. Schopf et al. (1975) have argued that groups with simple morphology are lumped by taxonomists because their strictly average genetic diversity produces a smaller array of phenotypic structures for taxonomic distinction. Corals have simple and highly plastic morphologies—a taxonomist’s nightmare and a sure prescription for lumping. Their genetic diversity may equal or exceed that of mammals for all we know. On the other hand, we may be quite sure that mammals and ammonites are oversplit at the family level—ammonites for their stratigraphic utility as Mesozoic guide fossils, mammals because we tend to make finer distinctions among animals that look more and more like us.

2. Differences among taxonomic levels.

Several consistent differences among taxonomic levels are more relevant to this study because their explanation must invoke a change in probability of branching and extinction. These changes are the basis for our

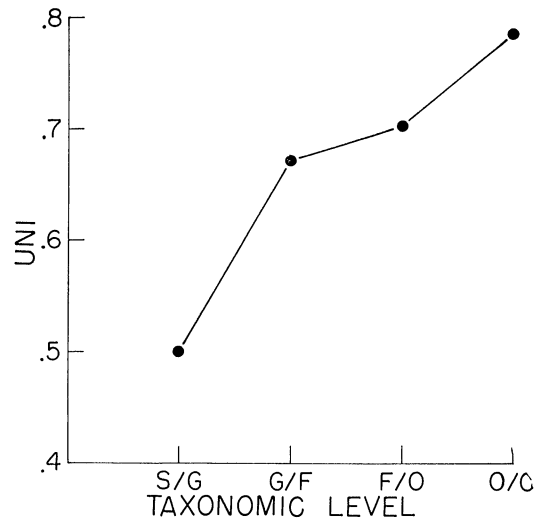


FIGURE 7. Rising values of UNI (uniformity) at higher levels of the taxonomic hierarchy (i.e. at decreasing probabilities for branching and extinction of taxa). S/G: species within genera, for diatoms only from Small, 1945. G/F: genera within families for all groups in Table 2. F/O: families within orders for all groups in Table 2. O/C: orders within classes from Table 2. These values include extinct and extant clades together.

distribution of clade statistics in the stochastic system.

We noted, for example, that mean UNI is high at low probabilities for branching and extinction—as the chance for long, parallel-sided clades increases. We may be confident that decreasing probabilities also characterize rising taxonomic levels; the chance of evolving a new order within any unit of time is far less than that for evolving a new species. If these probabilities control UNI, as the stochastic simulations suggest, then UNI should rise as we generate clades at successively higher taxonomic levels. Figure 7 displays this consistently rising UNI for the total samples (extinct and extant clades) of genera within families, families within orders and orders within classes. We also include a single (perhaps unrepresentative) point for species within genera. It portrays the only consistent data we could find at this level—species in extant genera of diatoms (Small 1945). We may need to reach the species level itself before we encounter branching and extinction probabilities sufficiently high to bring our expected value of UNI near 0.5.

## How to Detect Differences Between Real and Random Clades

We may search for differences between measures of real and random clades with three criteria:

i) For non-dimensional measures of shape, we may compare actual values directly—CG and UNI. Regardless of its size, scaling, number of intervals and diversity, a clade that is widest at the midpoint of its duration still has a CG of 0.5.

ii) For dimensional measures of size (SIZE, DUR and MAX DIV), we do not know how to circumvent the problem of scaling in making direct comparisons. We cannot contrast a computer simulation with 115 idealized time units and an equilibrium diversity set at 30 (or some other number of) coexisting lineages with a real world of 77 disparate intervals and a different limit (if any) on diversity. We have therefore compared differences between extinct (E) and extant (A, for alive) clades in the real world and in the simulations. These comparisons are dimensionless ratios.

iii) We compare the structure of correlation among clade statistics and variation within them for the real and random worlds (correlation matrices and tables of dimensionless coefficients of variation).

How different, then, is the real world from the stochastic system? How, in other words, is the real world “taxonbound” and “timebound”—i.e., in need of specific, causal explanations involving uniquenesses of time and taxon at various stages of earth history. The answer would seem to be “not very”—the outstanding feature of real and random clades is their basic similarity. Nonetheless, we find three possible cases of potential difference:

### A (Alive) Clades Larger Than E (Extinct) Clades

Differences in correlation matrices for statistics of real and random clades point to an important distinction in the formation of clade sizes. In the computer generated phylogenies, clades are defined by a criterion of minimum size. Variation in SIZE is necessarily modest (coefficients of variation range from 23.8 to 31.2 over the range of extinction

and branching probabilities used in the simulations). “Forced” correlations also arise: MAX DIV, for example, is negatively correlated with DUR ( $r$  ranges from  $-.242$  to  $-.421$ , invariably significant for sample sizes of greater than 100 clades)—with a strong constraint on SIZE, short clades (low DUR) will tend to be wide at their maxima (high MAX DIV) in order to reach the minimum size for status as a clade. Real clades, on the other hand, display an enormous variation in SIZE, with average coefficients of variation 4 to 5 times higher than those for stochastic clades. They are weakly constrained by a “canon of art” in conventional taxonomy very similar to the criterion of minimum size in the stochastic system—i.e., most taxonomists are uncomfortable with very large or very small clades: they are forever trying to break up large ones and amalgamate small ones with their nearest relatives. But this weak constraint does not overcome the fact that real clades are defined largely by morphology, and that successful morphologies tend to form long *and* diverse clades. In the real world, DUR and MAX DIV tend to be positively correlated ( $r = .255$  for orders within classes of 109 animal groups, not including Holocene records. This value of  $r$  is significant at the 1% level).

When we compare the SIZE of E and A clades in the stochastic system, we find that A clades are invariably larger than E clades (mean A/E ranges from 1.07 to 1.27 in the DE model). This difference arises because clades are defined only after the entire tree has been simulated. Early (i.e. extinct) clades are easily driven towards their minimum size because later branching provides so many opportunities for assigning subclades to later, descendant clades. But A clades provide few opportunities for dispersal of subclades; the subclades are too small to form their own clades, but they have no posterity for alternate attachment.

Table 2 shows that E clades are also smaller than A clades in the real world. But the effect is greater (average A/E is 6.8 for orders within classes, 2.2 for families in orders, and 1.8 for genera in families compared with a maximum difference of less than 30% for stochastic A and E clades). (We are aware that this accentuated difference is

TABLE 2. Mean values for statistics of real clades.

|                                | N<br>(extinct, alive) | SIZE    |        | MAX DIV |       |         |       |
|--------------------------------|-----------------------|---------|--------|---------|-------|---------|-------|
|                                |                       | Extinct | Alive  | Extinct | Alive |         |       |
| I. Orders Within Classes       | (45,99)               | 178.6   | 1219.4 | 1.84    | 5.76  |         |       |
| II. Families Within Orders     |                       |         |        |         |       |         |       |
| 1. Archaeocyathids             | (9,0)                 | 165.3   |        | 9.33    |       |         |       |
| 2. Coelenterates               | (20,17)               | 360.3   | 379.4  | 3.30    | 2.88  |         |       |
| 3. Bryozoans                   | (3,3)                 | 959.0   | 2799.7 | 7.33    | 26.33 |         |       |
| 4. Brachiopods                 | (9,5)                 | 1136.8  | 1206.4 | 8.78    | 5.80  |         |       |
| 5. Trilobites                  | (7,0)                 | 859.4   |        | 13.43   |       |         |       |
| 6. Echinoderms                 | (32,23)               | 363.3   | 733.6  | 3.88    | 4.61  |         |       |
| 7. Graptolites                 | (6,0)                 | 249.2   |        | 3.83    |       |         |       |
| 8. Fishes (excluding teleosts) | (26,13)               | 136.9   | 402.1  | 2.11    | 3.36  |         |       |
| 9. Birds                       | (5,28)                | 31.6    | 109.1  | 1.60    | 4.40  |         |       |
| III. Genera Within Families    |                       |         |        |         |       |         |       |
| 1. Corals                      | (48,18)               | 469.6   | 600.2  | 7.56    | 8.00  |         |       |
| 2. Brachiopods                 | (185,18)              | 244.8   | 436.9  | 4.49    | 5.72  |         |       |
| 3. Archaeogastropods           | (58,21)               | 325.6   | 565.1  | 3.16    | 7.39  |         |       |
| 4. Bivalves (clams)            | (87,77)               | 271.8   | 556.7  | 3.93    | 6.90  |         |       |
| 5. Nautiloids                  | (105,1)               | 186.3   | 388.0  | 5.00    | 3.00  |         |       |
| 6. Ammonites                   | (190,0)               | 83.7    |        | 6.22    |       |         |       |
| 7. Trilobites                  | (138,0)               | 242.0   |        | 6.59    |       |         |       |
| 8. Ostracodes                  | (68,36)               | 255.6   | 552.2  | 3.84    | 5.52  |         |       |
| 9. Cystoids                    | (22,0)                | 110.1   |        | 2.64    |       |         |       |
| 10. Echinoids                  | (40,47)               | 166.9   | 282.7  | 3.51    | 5.46  |         |       |
| 11. Graptolites                | (26,0)                | 207.5   |        | 4.92    |       |         |       |
| 12. Mammals                    | (137,120)             | 65.7    | 90.8   | 4.20    | 6.95  |         |       |
|                                |                       |         |        |         |       |         |       |
|                                |                       | DUR     |        | CG      |       | UNI     |       |
|                                |                       | Extinct | Alive  | Extinct | Alive | Extinct | Alive |
| I. Orders Within Classes       |                       | 121.4   | 396.6  | .491    | .539  | .889    | .717  |
| II. Families Within Orders     |                       |         |        |         |       |         |       |
| 1. Archaeocyathids             |                       | 24.0    |        | .496    |       | .834    |       |
| 2. Coelenterates               |                       | 129.1   | 169.6  | .492    | .522  | .741    | .844  |
| 3. Bryozoans                   |                       | 260.7   | 343.0  | .400    | .581  | .463    | .532  |
| 4. Brachiopods                 |                       | 182.9   | 444.2  | .477    | .492  | .699    | .517  |
| 5. Trilobites                  |                       | 153.1   |        | .410    |       | .558    |       |
| 6. Echinoderms                 |                       | 118.8   | 309.5  | .485    | .535  | .739    | .635  |
| 7. Graptolites                 |                       | 83.5    |        | .459    |       | .739    |       |
| 8. Fishes (excluding teleosts) |                       | 62.0    | 202.7  | .503    | .545  | .880    | .722  |
| 9. Birds                       |                       | 25.0    | 46.2   | .507    | .550  | .887    | .733  |
| III. Genera Within Families    |                       |         |        |         |       |         |       |
| 1. Corals                      |                       | 114.3   | 132.9  | .484    | .603  | .606    | .567  |
| 2. Brachiopods                 |                       | 81.4    | 171.4  | .491    | .530  | .728    | .620  |
| 3. Archaeogastropods           |                       | 155.8   | 138.8  | .491    | .557  | .679    | .552  |
| 4. Bivalves (clams)            |                       | 106.2   | 168.5  | .507    | .566  | .718    | .592  |
| 5. Nautiloids                  |                       | 58.0    | 203.0  | .486    | .548  | .722    | .637  |
| 6. Ammonites                   |                       | 22.4    |        | .489    |       | .762    |       |
| 7. Trilobites                  |                       | 52.2    |        | .495    |       | .780    |       |
| 8. Ostracodes                  |                       | 111.8   | 208.4  | .478    | .558  | .677    | .611  |
| 9. Cystoids                    |                       | 54.6    |        | .488    |       | .789    |       |
| 10. Echinoids                  |                       | 77.3    | 94.6   | .508    | .522  | .694    | .664  |
| 11. Graptolites                |                       | 55.8    |        | .489    |       | .767    |       |
| 12. Mammals                    |                       | 22.6    | 25.9   | .496    | .549  | .757    | .625  |

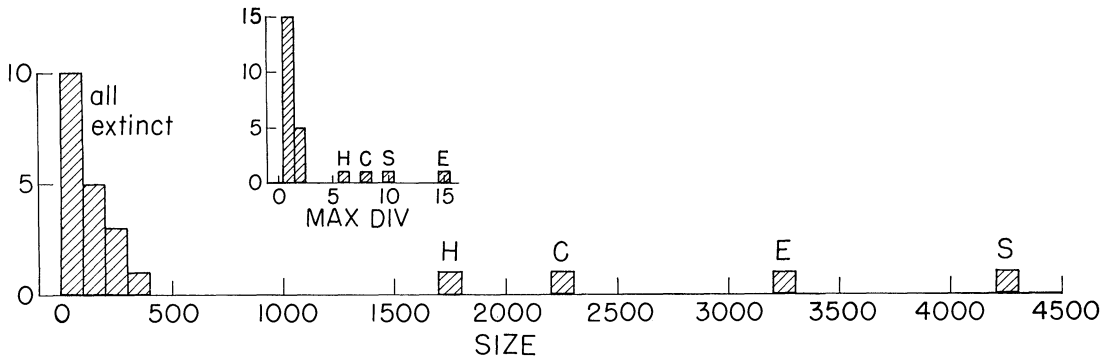


FIGURE 8. Frequency distribution of echinoderm orders for SIZE and MAX DIV to show great difference in size between extinct and alive clades. Living clades as follows: H, Holothuroidea; C, Crinoidea; E, Echinoidea; S, Stelleroidea.

largely an artifact of our partly arbitrary rule of decision for the stochastic system. Once we choose to define all clades by minimum size, E and A clades cannot differ by very much.)

We may be tempted to ascribe these differences between E and A clades to a non-random effect; but we cannot be sure whether the explanation reflects a basic pattern of evolution, or merely an imperfect fossil record. By definition, A clades have the bulk of their history near the present day, where chances of preservation are best; many E clades lived early in the history of life, and have suffered more from the ravages of metamorphism, burial and erosion. (We have removed all Holocene records from our calculation of A clades, so the added effect of maximal, modern preservation does not enter into our calculations.) Nonetheless, the effect may be too large and consistent to attribute to imperfection of the fossil record alone (for several groups, average A clades have as ancient an origin as average E clades).

Consider, for example, orders within classes for mollusks and echinoderms (Figure 8). These phyla either experienced their basic radiation during the lower Paleozoic, or else preserved its Precambrian products as skeletonized lower Paleozoic taxa. Here we see the pattern of "early experimentation and later standardization" that characterizes most adaptive radiations of major groups. These groups invade a previously "empty" ecological space (or quickly preempt earlier occupants), and proceed to develop an enormous number of fundamental variations at high taxonomic levels upon the same basic design. Most of

these early experiments are unsuccessful and quickly weeded out. We recognize them as higher taxa of limited duration and small membership—i.e., they are small E clades. A small subset of experiments persists, diversifies and achieves what can only be termed a kind of immortality (barring really major environmental catastrophe)—i.e., they become large A clades. A deterministic account must then invoke the morphologist's faith that superior ecological or structural design must have something to do with success of this magnitude. For orders within classes, the average echinoderm A clade is 27.1 times as large as an average E clade (2868 at  $N = 4$  vs. 106 at  $N = 19$ ). The frequency distribution of size (Figure 8) shows no overlap between E and A clades (Blastoidea, the largest E clade has a SIZE of 390; Holothuroidea, the smallest A clade, measures 1756). Lest SIZE seem an unfair and somewhat circular measure for this claim (since it includes clade length (DUR) and A clades are likely to be long), we point out that distributions of MAX DIV are equally non-overlapping (see inset of Figure 8). All E clades contain 1 or 2 orders at their maximum diversity, while the least diverse A clade (Holothuroidea) has a MAX DIV of 6 (the average A clade has a MAX DIV 8.1 times as great as the average E clade).

We have told a plausible story in the deterministic mode. It holds that the real world is "taxonbound"—superior designs tend to persist, diversify, and survive as large A clades.

Paleontologists (and evolutionary biologists

TABLE 3. Relative size of A and E clades in minimum-size and random-originator taxonomies. (Note that A/E ratios in the R-O model are as high as those observed in the real world.)

| Prob-<br>ability | DE Model     |       |      |                   |      |       | FF Model     |       |      |                   |      |       |
|------------------|--------------|-------|------|-------------------|------|-------|--------------|-------|------|-------------------|------|-------|
|                  | Minimum-Size |       |      | Random-Originator |      |       | Minimum-Size |       |      | Random-Originator |      |       |
|                  | A            | E     | A/E  | A                 | E    | A/E   | A            | E     | A/E  | A                 | E    | A/E   |
| .025             | 190.6        | 150.4 | 1.27 | 285.7             | 57.7 | 4.95  | 158.9        | 131.2 | 1.21 | 188.1             | 67.7 | 2.78  |
| .05              | 168.0        | 156.9 | 1.07 | 388.7             | 20.4 | 19.05 | 168.6        | 142.7 | 1.18 | 268.8             | 33.8 | 7.95  |
| .10              | 176.7        | 146.8 | 1.20 | 798.5             | 28.0 | 28.52 | 166.2        | 147.2 | 1.13 | 307.0             | 77.3 | 3.97  |
| .20              | 169.5        | 139.6 | 1.21 | 721.3             | 29.1 | 24.79 | 191.4        | 139.3 | 1.37 | 793.4             | 28.3 | 28.04 |
| .40              | 159.9        | 133.6 | 1.20 | 598.4             | 47.5 | 12.60 |              |       |      |                   |      |       |

in general) are famous for their facility in devising plausible stories; but they often forget that plausible stories need not be true. In this case, we accepted the magnitude of a difference in size between A and E clades as *prima facie* evidence for the structural superiority of extant designs. The absence of such a difference in random clades seemed to bolster our confidence in this traditional interpretation. Yet our random clades are defined by a criterion of minimum size that guarantees a strictly limited range of variation among them.

A stochastic tree can be divided into clades according to many criteria, not only the rule of minimum size employed so far. We therefore divided the same trees into the same number of clades according to a different algorithm—to obtain a “random-originator” rather than a “minimum-size” taxonomy. In this algorithm:

i) The initial lineage must be the originator of a clade (this is true in the minimum-size system as well).

ii) If the minimum-size criterion yielded  $n$  clades, then  $n-1$  random-originator clades are produced by randomly designating  $n-1$  lineages as ancestors of clades.

iii) All undesignated lineages are allocated in such a way that resulting clades are monophyletic (*sensu lato*—i.e., including paraphyletic clades).

The resulting differences in size between A and E clades fully match the discrepancy between real A and E clades (Table 3). E clades in the random-originator system tend to be very small because tiny twigs without descendants are often chosen under rule (ii). Some A clades are small for the same reason (living twigs), but others are immense since they include the persisting main trunk pruned

of a few twigs and branches. Thus, A clades in the random-originator system are larger than E clades to the same or greater extent than in the real world.

This successful simulation does not invalidate the deterministic hypothesis of structural superiority (among the five authors of this paper, some support it by intuition while others do not). But it does demonstrate that a belief in structural superiority requires some more evidence than a simple pattern of diversity; the same pattern arises if taxonomists work by an algorithm closer to our random-originator than to our minimum-size criterion for selecting clades. (We speak here not of differing patterns in evolution, but of taxonomic practice. We have partitioned the same evolutionary trees by both criteria.)

The random-originator algorithm also removes another argument for uniqueness in real clades. Minimum-size clades have much lower coefficients of variation than real clades, but random-originator clades exceed real clades in CV (Table 3). Real clades are now bracketed by two systems for taxonomizing a stochastic tree. This finding may provide some insight into taxonomic practice. Conventional taxonomy works by a criterion of art that values balance in the sizes of groups. This criterion yields clades less variable in size than our random-originator clades, but its dictates are not sufficiently strong to reach the restricted variability of our minimum-size clades.

### Low Values of UNI for Clades of Wide Taxonomic Separation

In the damped-equilibrium model, we have been unable to simulate average values of UNI much below 0.5 (i.e., clades of highly

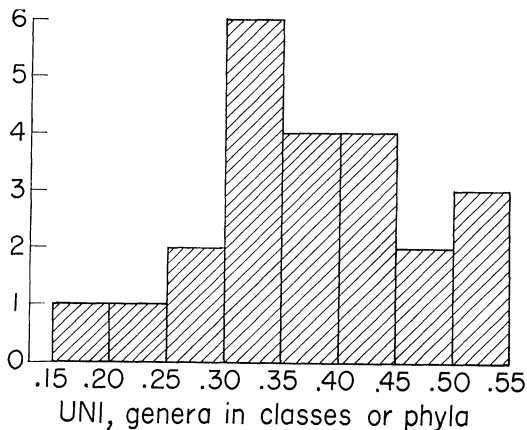


FIGURE 9. Frequency distribution for UNI (uniformity) at the level of genera within classes or phyla. Data calculated from charts of Müller, 1961. Groups include radiolarians, foraminiferans, echinoids, ostracodes, fishes, amphibians, reptiles, birds, mammals, sponges, bryozoans, gastropods, nautiloids, dibranchiate cephalopods, bivalves, ammonites, trilobites, graptolites, scleractinian corals, rugose corals, tabulate corals, malacostracans, and inarticulate brachiopods.

fluctuating diversity that fill less than half their circumscribed rectangle). High values of UNI also characterize all our data for clades constructed by including lineages within the next higher taxonomic rank. We argued previously that these high values of UNI are largely the result of generally low probabilities for branching and extinction of taxa.

But another method of tabulation offers an opportunity for studying UNI at greatly increased probabilities. If we consider the lowest practical taxonomic level (genera) within clades of the highest (classes or phyla), we maximize the opportunity for rapid fluctuations in diversity. We therefore calculated UNI for Müller's (1961) clades of genera within classes or phyla. For 23 clades, mean UNI is .380; the frequency distribution of Figure 9 shows only three groups with UNI greater than 0.5 (ostracodes, and rugosan and scleractinian corals).

An interesting confirmation of these low values arises from a separate analysis of species-level data in post Paleozoic echinoids (Raup 1975). Mean UNI for species within 59 families is .334. [We used only extinct clades with durations of 3 or more stratigraphic units. UNI is constrained by its definition as the percentage of a circumscribed

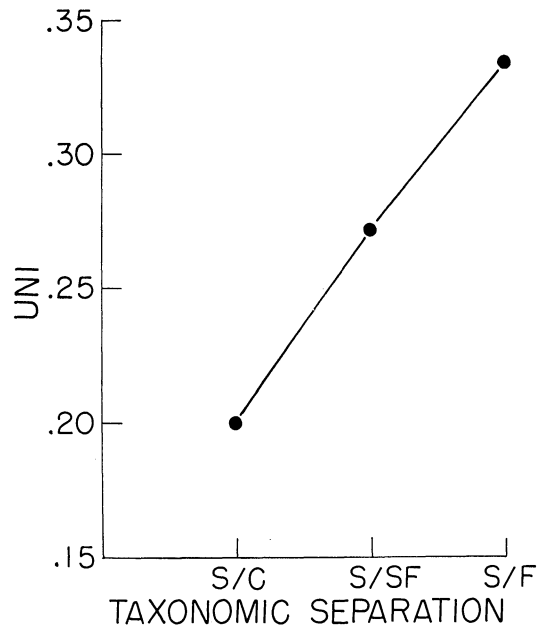


FIGURE 10. Rising values of UNI (uniformity) for decreasing taxonomic separation in clades of echinoid species. S/C, species in classes; S/SF, species in superfamilies; S/F, species in families.

rectangle filled by a clade, to be 1.0 for clades of 1 unit, and greater than 0.5 for clades of 2 units (the unit of greatest diversity fills half the rectangle, and the second unit must fill some of the remaining space). As duration increases, possible minimum values of UNI decrease, though upper values of 1.0 are always attainable (long, parallel sided clades). We chose 3 as the minimum number of units, because this is the first duration that permits a value of UNI below 0.5.] Moreover, we can calculate UNI for greater taxonomic separations within the same data. The value steadily decreases as taxonomic separation increases (.271 for species within 19 superfamilies and .199 for species within the entire class—Figure 10).

One possibility is that these low values might only be the result of separating clades by several taxonomic levels, and that a similar separation in stochastic clades might also drive mean UNI far below 0.5. But it does not. For 7 separate runs of the damped equilibrium system at branching and extinction probabilities of 0.1, we constructed a third taxonomic level by dividing the clades into three monophyletic higher groups ("superclades"). Our three levels are, then, lineages,

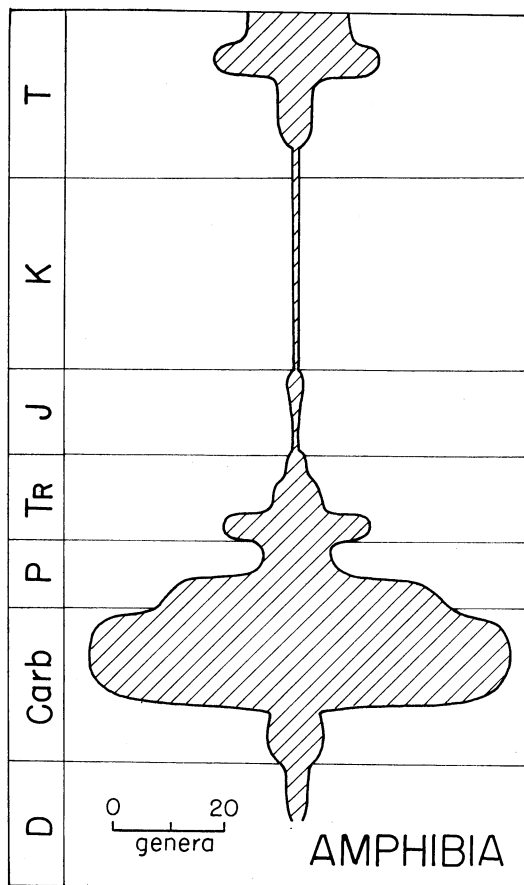


FIGURE 11. Clades for genera within classes for amphibians. Redrawn from Müller, 1961.

clades ( $N = 143$ ) and superclades (3 superclades per run). We calculated mean UNI for lineages within superclades (level 1 within level 3) to see if values dropped below 0.5 with increasing taxonomic separation. For 21 superclades (3 in each of 7 runs), mean UNI is 0.49.

Low values of real UNI may represent a non-random effect. But we again have the problem of deciding whether it reflects a pattern of evolution or the imperfections of the fossil record. UNI, as we noted before, is highly sensitive to the maximum diversity that sets one dimension of the circumscribed rectangle. If maximum diversity is primarily a function of unusually excellent preservation during a certain time period, then the effect may be artificial (the correlation of exuberant diversity for Mississippian crinoids with vast deposits of shallow-water limestones in the

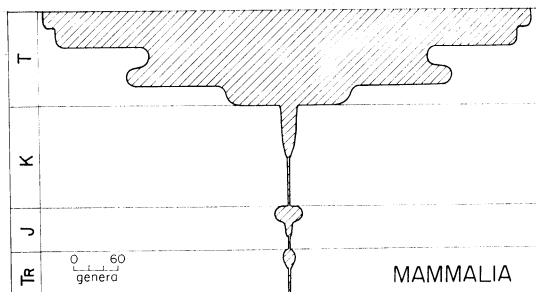


FIGURE 12. Clades for genera within classes for mammals. Redrawn from Müller, 1961.

American continental interior provides a classic example). But a biological consideration in several specific cases may argue for a deterministic effect. Consider the clades of genera within classes for amphibians and mammals (Figures 11 and 12). The early Carboniferous was probably a "good" time for amphibians. Reptiles had not yet evolved and the vertebrate, terrestrial world belonged to amphibians alone. Things have not been the same since reptiles took over during the very next period. Amphibian UNI of .191 (the lowest value of Figure 9) may be a function of truly great Carboniferous diversity and an equally real subsequent, drastic and permanent reduction related to the evolution of "higher" vertebrate classes. The low UNI of mammals (.299) reflects their rapid Tertiary diversification following the extinction of dinosaurs at the close of the Cretaceous. But mammals, for most of their history, were a small group of small animals living in the interstices of a dinosaur's world. The great Tertiary diversification sets the width of the rectangle, but the very skinny Mesozoic portion of the clade drives UNI well below 0.5.

Thus, for both amphibians and mammals, low values of UNI are probably a result of real, biological interaction with other groups of vertebrates. The real world may be, in this respect, "timebounded." Some times really are "good" for certain groups (in these cases, because a successful competitor had either not yet evolved, or recently become extinct).

### CG Below 0.5 in E Clades

The average CG for E clades in 12 groups of genera within families is significantly less

TABLE 4. Values of CG for early and later arising E clades. <sup>1</sup>Sample sizes designated as (total: early arising, later arising); <sup>2</sup>pre Arenig vs. Arenig and later; <sup>3</sup>pre Middle Ordovician.

|                                       | Cambrian-<br>Ordovician | Silurian<br>and later   |
|---------------------------------------|-------------------------|-------------------------|
| Brachiopods (185:81,104) <sup>1</sup> | .474                    | .500                    |
| Graptolites <sup>2</sup> (26:10,16)   | .460                    | .508                    |
| Bivalves (87:17,70)                   | .500                    | .510                    |
| Paleozoic Corals (36:10,26)           | .476                    | .497                    |
| Archaeogastropods (58:24,34)          | .481                    | .498                    |
| Ostracodes (68:32,36)                 | .471                    | .485                    |
| Trilobites <sup>3</sup> (138:124,14)  | .488                    | .519                    |
| Nautiloids (105:55,50)                | .485                    | .487                    |
| Total (703:353,350)                   | .482                    | .499                    |
|                                       | <u>Paleocene</u>        | <u>Eocene and later</u> |
| Tertiary Mammals (124:40,84)          | .474                    | .508                    |

than 0.5. At first glance, this appears to represent an important difference between real and random worlds; we cannot generate mean CG lower than 0.5 in a truly stochastic system (where CG of the idealized diamond is exactly 0.5). It would seem that an average real clade tends to be wide at its bottom because it radiates rapidly following the invasion of new ecological space or the evolution of new morphological designs by ancestral lineages. After stabilizing at some maximum diversity, it then tends to peter out more slowly, forming an attenuated upper part. The random model seems to be violated in a fundamental way: all times are not alike to members of a clade if chances for diversification are characteristically greater during their early history.

But we then divided E clades within each group into those arising during the Cambrian or Ordovician periods and those arising later. We have no evidence for any complex animals much below the base of the Cambrian. The famous Cambrian "explosion" marks a rapid phase of skeletonization for nearly all invertebrate phyla with important fossil records. The Cambrian and Ordovician periods record the initial radiation and diversification of complex animal life in the oceans—the original filling up of the ecological barrel, so to speak. By the beginning of Silurian times, all major organic designs were established; evolution since then has been largely the story of endless variation upon these set themes.

We detect a consistent pattern for the 8 groups with sample sizes large enough for meaningful comparisons (N of 10 or more in each category). In all cases (Table 4), mean CG for Cambro-Ordovician clades is lower than for Silurian and later clades. Though the differences are not always significant (as, obviously, for nautiloids), the pattern is unerringly the same. There are no exceptions. Moreover, we see that the combined mean values of less than 0.5 are due entirely to the low CG's of the Cambro-Ordovician clades. Only these early clades have the wide bottoms of groups that radiate rapidly during their initial history. Silurian and later clades are as close to the idealized, equilibrational 0.5 as anyone could hope (0.4993 for 350 clades).

Is this early non-equibrational phase a general feature of the evolutionary process, or merely a time-specific event in the early evolution of complex, marine life. Fortunately, we have an independent test. Mammals filled their ecological barrel following the extinction of ruling reptiles at the close of Cretaceous times: small mammals of restricted diversity found an "empty" world depopulated of its formerly dominant vertebrates; they radiated spectacularly during subsequent Paleocene times. The Paleocene for mammals should be like the Cambro-Ordovician for marine invertebrates, while Eocene and later times might be as equilibrational for mammals as Silurian and later periods have been for marine invertebrates. We are delighted to report that mean CG for clades originating in the Paleocene is .474 (N = 40); it is .508 (N = 84) for Eocene and later E clades (Table 4). [It is interesting to note that colonization of sterile habitats in ecological experiments generally proceeds very quickly to maximal, above-equilibrium diversity, presumably as a response to an empty ecological barrel. Diversity then falls back to a very long-lasting equilibrium level; this is the precise analog in ecological terms of a clade with low CG (Simberloff 1974)].

We do not regard these low CG's for clades originating during the early history of larger groups as discordant with patterns in the random simulations. Equilibrium cannot be achieved all at once; an initial period of rapid expansion from an origin at restricted



diversity to equilibrium must be different from subsequent life at stochastic equilibrium. In particular, probabilities for branching must exceed those for extinction during this initial, expanding phase. It is more important to note that this early phase is quickly finished, and that the bulk of mammalian or marine invertebrate history has occurred in the subsequent, equilibrated period. In fact, we mimicked this process in the preequilibrium phase of our DE model. Since we began with a single lineage, our damping function guaranteed that branching probabilities would exceed extinction probabilities until equilibrated diversity was reached. Moreover, we have already noted (p. 28) that mean CG for simulated clades originating in this early preequilibrium phase is less than 0.5, while equilibrium clades never fall below 0.5. The explanation for Cambro-Ordovician invertebrates and Paleocene mammals must be the same: origination rates exceeded extinction rates as the world filled up. Our DE model seems to simulate the real world and we can understand its behavior thereby.

Cambro-Ordovician times (Paleocene times for mammals) mirror our preequilibrium phase. Origination rates were high as the ecological barrel filled up. But for the long stretch of Silurian to Recent times, despite mass extinction and bursts of origination, the world's clades have been in equilibrium for CG.

Charles Lyell, conventional hero in the history of geology, held as his most cherished belief a notion that would embarrass most of his modern champions if they knew about it (it was quietly buried long ago as unfit for candidates to "sainthood"). Lyell believed that earth history, like planetary motion, was in a dynamic steady state: seas moved in and out, continents grew and foundered, but the earth remained essentially the same: species arose and disappeared, but the average complexity of life did not change. This belief represents one extreme metaphor in a continuum that places directionalism and notions of inherent progress at the other pole. The historical bias of paleontologists has led to a strong affinity for this opposite pole—assertions of inherent uniqueness for each period of time and to the search for "directions" in earth history. We, on the other hand, believe

that Lyell's metaphor is due for a renaissance and that the post-Ordovician mean CG of 0.5 offers a powerful case for its importance.

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