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Source: *BioScience*, Vol. 28, No. 4 (Apr., 1978), pp. 277-281

Published by: American Institute of Biological Sciences

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Generality and Uniqueness in the History of Life:

An Exploration with Random Models

Stephen Jay Gould

Paleontologists operate in a perpetual Catch-22. We study the most complex events in biology over the broadest ranges of time and space. We uncover various patterns in the history of life, and we wish to measure the multitude of influences that produce them. But we deal in frozen events long past. We can neither experiment nor manipulate; many forms of the past do not even have close analogs among the living. How then can we tease apart and measure the various inputs to provide materials for a theory of macroevolutionary change?

One strategy calls for the identification, measurement, and subtraction of general effects in order to identify the more specific causes of a pattern. In allometric studies, for example, we invoke basic geometry and physics to predict the effects of size itself. Larger mammalian bodies carry larger brains. Body size increased in human evolution, but the correlated rate of increase in brain size is vastly greater than the laws of scaling predict. Thus, unsurprisingly, our large brain records the operation of causes specific to our lineage, not merely the general effects of scale (Pilbeam and Gould 1974).

What general effect might we try to identify and subtract from the history of life? The patterns produced by random change should be our first consideration. (If we keep at it long enough, simple coin flipping will generate some impressive runs of heads or tails, taken by the uninitiated as a sure sign of causal order. And if the history of life provides anything, it has given us a multitude of flips.) No effect could be more general, for our stochastic models deny the uniqueness of time and taxon, which has served as a cornerstone for causal inference in pa-

leontology ("mammals are better at . . . than . . ." or "the Cambrian was a time of . . .").

On one hand, stochastic models are a criterion of subtraction for the identification of effects produced by conventional causes; on the other hand, they contain a potential seed for a radical interpretation of the history of life. Our faith in determinism is more a prejudice of thought than a documented truth. What if little or nothing is left after we perform the subtraction? Could there be a timeless generality behind the apparent uniqueness of events in the fossil record? Allometric studies often leave nothing after the subtraction of size. Irish elks did not have unusually large antlers; they had antlers just the "right" size for deer of their body size (Gould 1974).

THE MODEL

During the past five years, my colleagues D. M. Raup, T. J. M. Schopf, J. J. Sepkoski, Jr., D. S. Simberloff, and I have been exploring the consequences of stochastic models for the history of life (Gould et al. 1977, Raup and Gould 1974, Raup et al. 1973, Schopf et al. 1975). We have proceeded via simulation by computer. Our basic model generates an evolutionary tree in the following way: We begin with a single lineage and allow it (and any descendants) three options at each successive slice of time: it may persist unchanged, branch to produce two lineages, or become extinct. We equate the probabilities of branching and extinction and use a random number generator to specify the fate of each lineage at each time.

Actually, we begin with higher probabilities for branching than extinction; when diversity reaches a predetermined "equilibrium"—this happens very early in the simulation—we equate branching and extinction. If standing diversity strays too far from this equilibrium, we

damp the system back towards it by raising the probability of extinction if diversity gets too high or augmenting the chance of origination if it falls too low. We call this the "damped-equilibrium" model. We also use a "freely floating" model with no equilibrium diversity, no preequilibrium phase at the beginning, and no damping. These runs often abort and occasionally explode, but their patterns are not much different from the damped-equilibrium runs (see Gould et al. 1977).

The result of this simulation is an evolutionary tree, often copiously branched. We proceed, as a paleontologist would, to taxonomize the tree into a series of larger monophyletic branches, or "clades." (In the absence of morphology, we use monophyly and minimum size as criteria for the identification of clades. We have also worked with stochastic simulations of morphology [Raup and Gould 1974].) Finally, we follow conventional practice and depict the clades as a series of "spindle diagrams," portraying the history of fluctuations in abundance for each clade through time. As an initial gestalt, these random clades look strikingly like real ones (Fig. 1).

To venture beyond this visual impression, we developed a set of "clade statistics" for comparing real with random clades (Fig. 2). We tried to measure the various properties used by paleontologists to assert causal order:

- *Measures of size:* DUR (duration, or time of existence), MAX DIV (maximum diversity, or greatest number of simultaneous lineages), and SIZE (a combined measure of persistence and diversity—each lineage contributes a unit to SIZE for each interval of time during which it lives). Causal assertions of superiority or inferiority are often based upon differences in relative size of clades.
- *Relative time of mean diversity:* CG (center of gravity). As Fig. 3 indicates,

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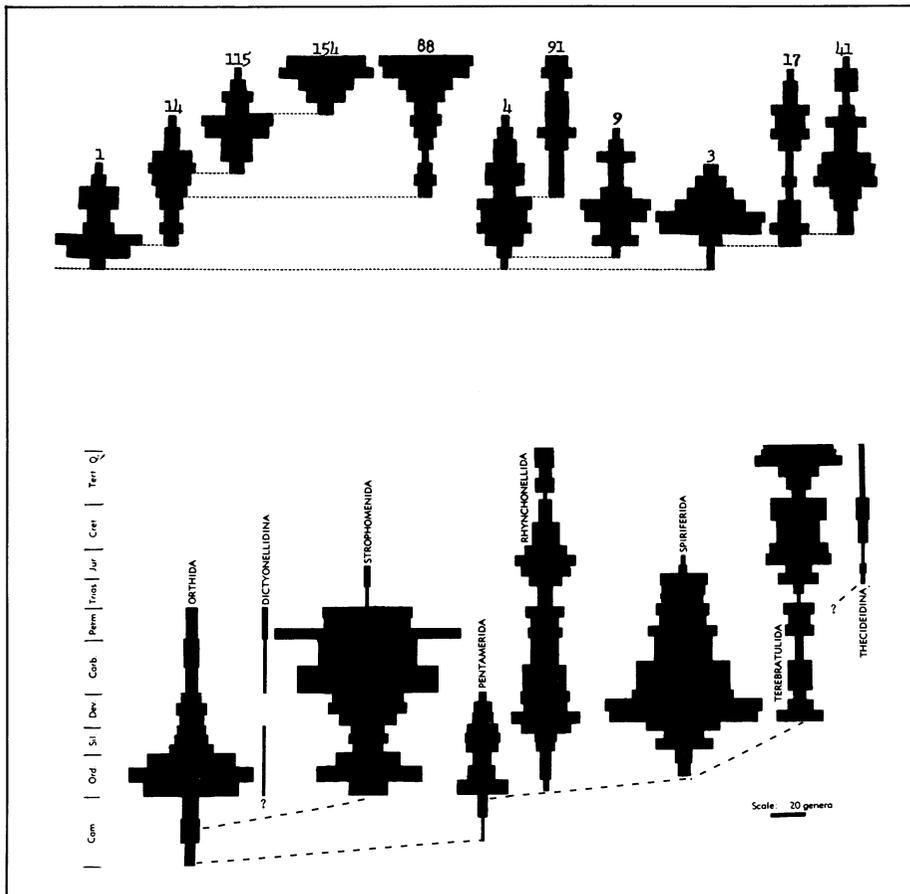


Fig. 1. Comparison of random with real clades. Top: clades for one run of the random program at branching and extinction probabilities of 0.1. Bottom: real clades for genera within orders of brachiopods.

clades with greatest diversity early in their history have CG less than 0.5; greatest diversity late in the clade's existence yields CG greater than 0.5. Causal assertions about adaptive radiation and patterns of extinction have often relied upon this aspect of clade shape.

• *Fluctuation in diversity*: UNI (uniformity). We circumscribe a rectangle about the clade and measure the percentage of area filled by the clade itself. Par-

allel-sided clades have high values of UNI; clades with marked fluctuations in diversity exhibit low values (Fig. 3). Causal assertions of relative fit to environment or of environmental fluctuations through time are often based upon fluctuations in clade diversity.

THE SPACE OF REAL CLADES

We computed these statistics for real clades at three taxonomic levels: genera within families (lowest possible, since species-level taxonomy is inconsistent and untabulated), families within orders, and orders within classes for all of life, prokaryote to hominid (see Gould et al. 1977, p. 30 for sources of data). It is not always easy to sort three major effects: (a) biases of an incomplete fossil record and inconsistent taxonomy; (b) differences based on taxonomic level; and (c) actual patterns in the history of life. Fig. 4, for example, summarizes all our data in the form of normalized varimax loadings for a Q-mode factor analysis of mean values within phyla (the three axes account for 98% of all information). High scores for CG and UNI dominate the

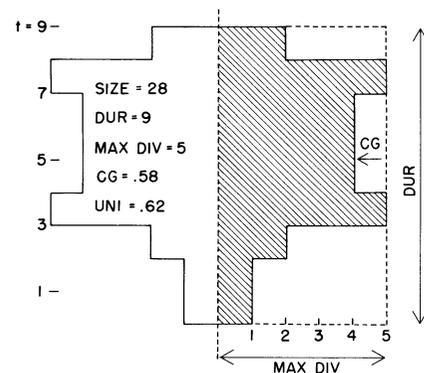


Fig. 2. Clade statistics used in this analysis. DUR = duration; MAX DIV = maximum diversity; CG = center of gravity; UNI = uniformity.

first axis (62%). Samples with high projections have maximum diversity after the midpoints of their existence and do not fluctuate much in diversity through time.

This is the dominant pattern among real clades at these high taxonomic levels (orders within classes for all of life loads most strongly on this axis). But we do not know whether it is an artifact of preservation (more fossils from more abundant and less altered rocks as we approach modern times) or a reflection of truly increasing diversity through time (see Raup 1972 vs. Valentine 1973). High scores for measures of size (SIZE, DUR, and MAX DIV) dominate the second axis (16.6%). Samples with high loadings have large clades. Clades for families within orders always load more strongly than clades for genera within families of the same phylum, and we detect an effect of taxonomic level. High scores for MAX DIV (positive) and DUR (negative) dominate the third axis (19.5%). Samples with high loadings have short and fat clades.

Since orders range longer than families, points for genera within families tend to load higher than points for families within orders (Fig. 4). But this effect of taxonomic level does not exhaust the difference of loading on the third axis and evolutionary rate in micromacarthurs (an inverse measure of extinction rate, see Van Valen 1973) for all samples at the level of genera within families. Rapid evolvers (ammonites and mammals in particular) have higher loadings, and this reflects a real pattern in the history of morphology (though not necessarily in corresponding genomes, see Schopf et al. 1975).

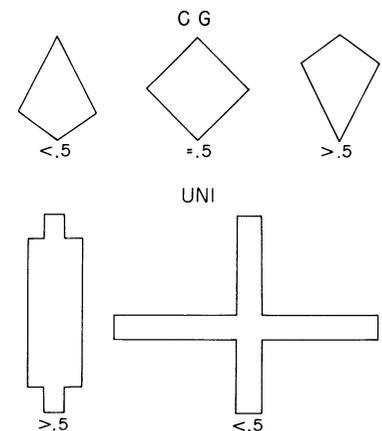


Fig. 3. Shapes of clades that yield high and low values of CG (center of gravity) and UNI (uniformity).

TABLE 1. Correlation between loading on third axis and evolutionary rate (based on extinction, from Schopf et al. 1975), $r = 0.89$.

Group	Loading on third axis	Evolutionary rate in micro-macarthurs
ammonites	.799	25
mammals	.639	30
trilobites	.577	15
nautiloids	.514	15
brachiopods	.424	15
corals	.416	10
echinoids	.390	10
bivalves	.349	8
ostracodes	.312	10
archaeogastropods	.220	4

We do not deny that the great Permian extinction had a deterministic cause peculiar to the circumstances of its time.

I illustrate our method of comparing real and random clades with our standardized measures of clade shape: UNI and CG. Fig. 5 shows the mean values of UNI for both "damped-equilibrium" and "freely-floating" models of the stochastic simulations over a wide range of probabilities for branching and extinction of lineages. The pattern is fairly simple and similar for the two models. Mean values of UNI lie near 0.5 at relatively high probabilities of branching and extinction (the idealized random clade is shaped like a diamond, and diamonds fill half their circumscribed rectangle). But, as we move to low probabilities of

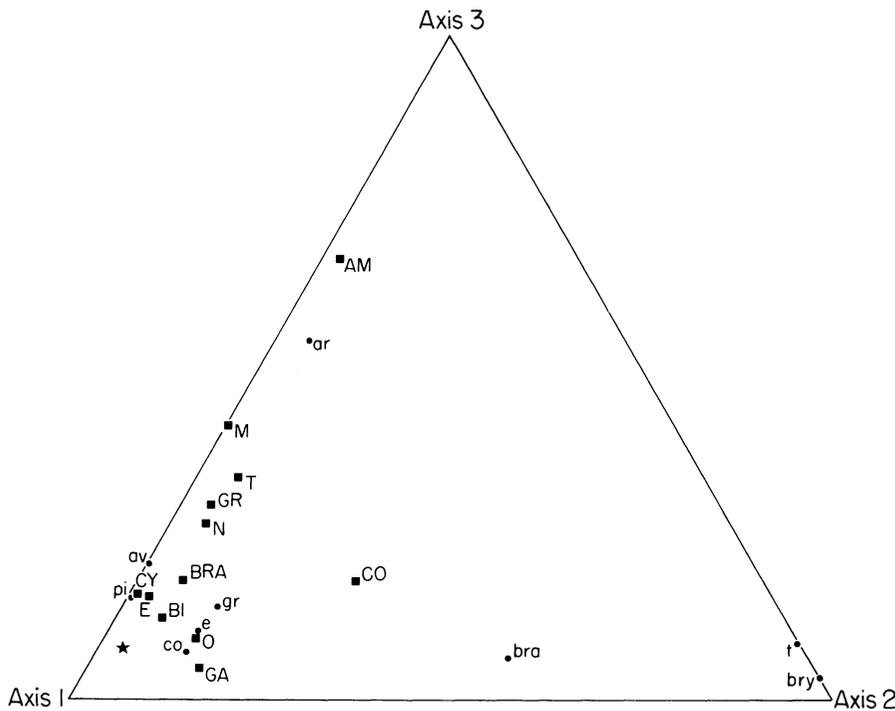


Fig. 4. Normalized loadings for taxonomic groups in 3-axis Q-mode varimax analysis. See text for interpretation. Squares and uppercase letters represent mean vectors for genera within families; points and lowercase letters for families within orders. The star represents orders in classes for all of life. AM, ammonites; ar, archaeocyathids; av, aves; BI, bivalves; BRA and bra, brachiopods; bry, bryozoa; CO and co, coelenterates; CY, cystoids; E and e, echinoids; GA, gastropods; GR and gr, graptolites; M, mammals; N, nautiloids; O, ostracodes; pi, pisces; T and t, trilobites.

COMPARISON OF REAL AND RANDOM CLADES

Intrigued as we are by the use of this method for sorting out differences among real clades, we are more impressed by its promise for assessing the potentially random component of real patterns. Here we compare the clade statistics of these real clades with average values for random clades generated over the entire reasonable range of probabilities for branching and extinction in our model. We have been struck throughout our work by the similarity in pattern between real and random. Little about the geometry of size and shape in real clades requires an explanation in conventional causal terms. To this strong statement, however, I quickly add two disclaimers: First, consistency with random generation does not prove the acausal status of a pattern, for conventional causes may yield the same result. It does demonstrate, however, that the assertion of cause cannot be based upon the apparent orderliness of geometric pattern alone, though paleontologists have usually done just this. Second, we consider here only the sizes and shapes of clades, not their relative position in geological time.

Thus, we do not consider such striking events as mass extinction, unless simultaneous disappearance is reflected in unusual shapes or sizes of the dying clades.

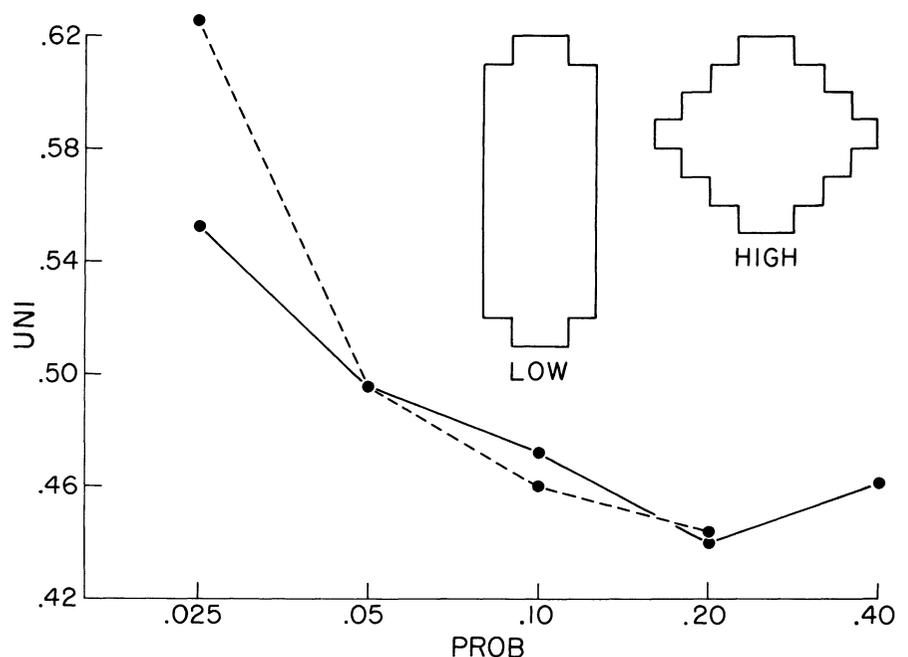


Fig. 5. Distribution of mean values for UNI (uniformity) at different probabilities of branching and extinction in the stochastic simulations. Solid line: damped equilibrium model. Dashed line: freely floating model. The inset shows average clades for low and high probabilities (abscissal values).

branching and extinction, mean values of UNI begin to rise, for now clades can be made of single lineages that persist long enough to reach minimal size for a clade (thanks to low probabilities for branching and dying). These single-lineage clades are parallel-sided and have a UNI of 1.0.

Thus, the random model suggests that patterns in UNI should reflect probabilities of branching and extinction. Real clades confirm this in a study of differences among taxonomic levels. As we move to the generation of higher taxonomic levels, probabilities should drop and UNI should rise. Fig. 6 affirms this pattern (see Gould et al. 1977 for details): Orders within classes for all of life, $N = 144$; families within orders for 9 groups, $N = 206$; genera within families for 12 groups, $N = 1442$. Data for species are harder to find, and the point records only a single group (perhaps unrepresentative), the diatoms. We can drive UNI below 0.5 by wider separation of taxonomic levels to increase still further the probabilities of branching and extinction. If we construct clades for species of echinoids, first in families, then in superfamilies, and finally in the entire class, UNI drops steadily from .334 (families at $N = 59$) to .271 (superfamilies at $N = 19$) to .199 (the class Echinoidea at $N = 1$). The species in a single family may not branch or die in any given interval, but the species of an entire class must undergo many events of origination and extinction in each period of time.

BURST AND EQUILIBRIUM IN MODEL AND WORLD

Fig. 7 shows mean values for CG in the stochastic simulations. For the damped-equilibrium model (solid line), mean CG rises above 0.5 at high probabilities of branching and extinction. The conventions of our simulation require that each clade begin as a single species; thus, each clade comes to a "point" at its origin (see inset on Fig. 7). But it may become extinct by simultaneous wipe-out of several lineages. Clades with pointed bottoms and flat tops due to simultaneous extinction have high values of CG. At low probabilities of branching and extinction, simultaneous wipe-out is rare and CG stays near 0.5; at high probabilities, flat tops occur more frequently and mean CG rises.

But how can CG ever get below 0.5? The answer is that it can't in a truly sto-

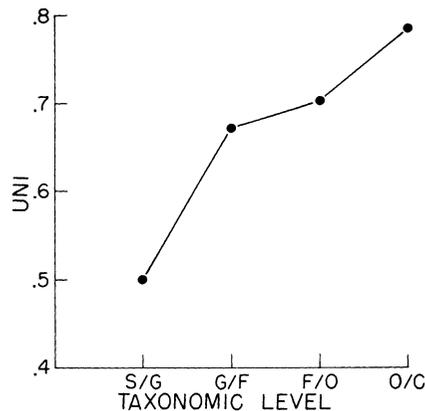


Fig. 6. Rising values of UNI (uniformity) at higher levels of the taxonomic hierarchy (i.e., at decreasing probabilities for branching and extinction of taxa). S/G: species within genera, for diatoms only. G/F: genera within families. F/O: families within orders. O/C: orders within classes.

chastic system that treats all times alike (indeed, CG never falls below 0.5 in the freely floating model). But the damped-equilibrium model includes an initial preequilibrium phase during which probabilities for origination exceed the chance of extinction. Clades that begin during this phase have an initial flowering produced by high rates of origination. But they peter out slowly during the subsequent period of lower and equal probabilities for branching and extinction. With fat bot-

oms and attenuated tops, these clades have mean values below 0.5. At low probabilities of branching and extinction in Fig. 7, the effect of flat tops due to simultaneous wipe-out (high CG) is weaker than the influence of low CG for clades originating in the preequilibrium phase. Hence, mean CG for all clades falls below 0.5. The drop below 0.5 must mark these preequilibrium clades because mean CG never falls below 0.5 if we consider only clades originating after probabilities of branching and extinction are equalized (dotted line of Fig. 7).

Real clades for genera within families show a striking similarity to stochastic clades in the damped-equilibrium model. The history of life included a preequilibrium phase marking the rapid transition from a world that had been dominated for three billion years by simple algae to our modern diversity of marine invertebrates.

If we divide the extinct clades of each group into those that originated during this preequilibrium phase (Cambrian-Ordovician) and those that began later (Silurian to Tertiary), we find a pattern without exception in eight groups (Table 2): Mean CG for Cambro-Ordovician clades is lower. The mean CG for 350 Silurian and later clades is 0.4993, as close to the idealized 0.5 (the equilibrium diamond) as anyone could hope; 353 pre-

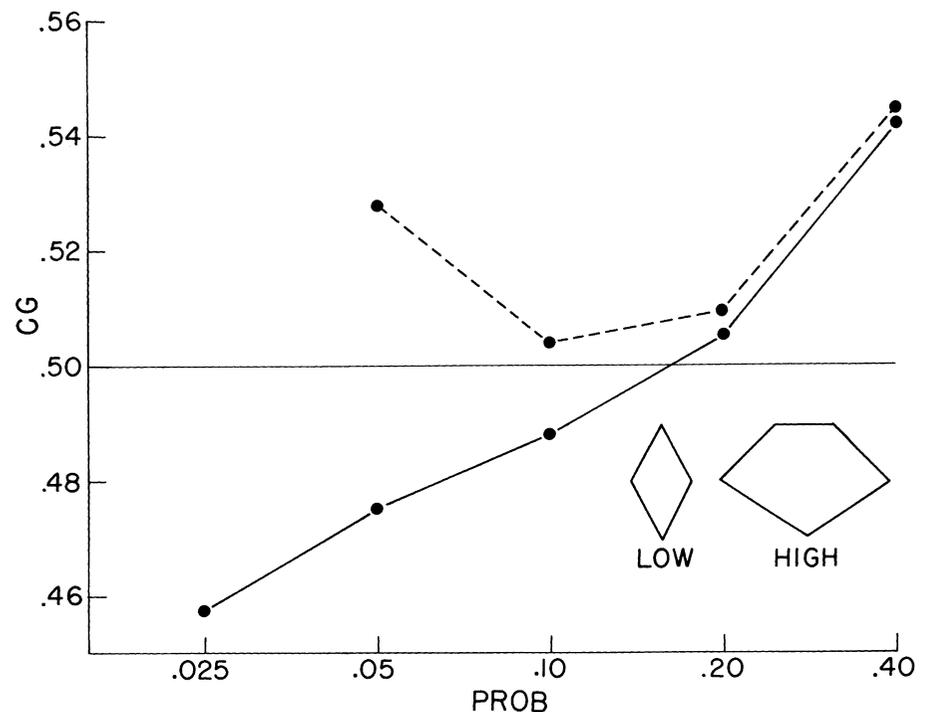


Fig. 7. Distribution of mean values for CG (center of gravity) at different probabilities of branching and extinction in the stochastic simulations. Solid line: damped equilibrium model for all extinct clades. Dashed line: damped equilibrium model for clades arising after the initial preequilibrium phase. The inset shows average clades for low and high probabilities (abscissal values).

TABLE 2. Values of CG for preequibrial and later clades.

Group	Silurian and later	
	Cambrian-Ordovician	
Brachiopods (185:81,104)*	.474	.500
Graptolites (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 (138:124,14)	.488	.519
Nautiloids (105:55,50)	.485	.487
Total (703:353,350)	.482	.499
		Eocene and later
	Paleocene	
Tertiary Mammals (124:40,84)	.474	.508

*Sample sizes designated as (total: early arising, later arising).

equibrial clades yield an average CG of 0.482.

Lest readers suspect that this pattern represents a peculiarity of marine invertebrates or lower Paleozoic times, and not a general property of systems in

sigmoidal growth, we have a confirming case from another system. Mammals passed their preequibrial phase on land during the Paleocene. Forty mammalian clades that began in the Paleocene yield a mean CG of 0.474. Average CG for 84 Eocene and later clades is 0.508.

Paleontologists have reveled in the particularity of their record. They have devoted lives to intense specialization on lower Permian brachiopods or mid-lower Jurassic ammonoids in the belief that historical uniqueness is irreducible. We do not deny either this uniqueness or the causal basis of events in the small (this brachiopod became extinct in that bay for a reason). But patterns at a larger scale may arise for other reasons or for no conventional reasons at all. Every flip comes up heads or tails for a reason (and we might know it if we could specify the complex and uncontrolled factors of original side up, height of flip, force of flip, height of hand catching flip, etc.). Still, a value near the stochastic 50-50 is a good prediction for a large sample. Silurian and later CG of 0.5, through all the epochs of mass extinction and drifting continents, provides an argument for stochastic timelessness in the history of life as well. True generality can exist amidst a plethora of particulars.

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