Asymmetry of Lineages and the Direction of Evolutionary Time

STEPHEN JAY GOULD, NORMAN L. GILINSKY, REBECCA Z. GERMAN

Evolutionary time has a characteristic direction as demonstrated by the asymmetry of clade diversity diagrams in large statistical samples. Evolutionary groups generally concentrate diversity during their early histories, producing a preponderance of bottom-heavy clades among those that arise early in the history of a larger group. This pattern holds across taxonomic levels and across differences in anatomy and ecology (marine invertebrates, terrestrial mammals). The quantitative study of directionality in life's history (replacing vague, untestable, and culturally laden notions of "progress") should receive more attention from paleobiologists.

DOES THE HISTORY OF LIFE EXHIBIT DIRECTIONAL OR "vectorial" properties? This issue has been a focus of contention ever since the beginnings of modern stratigraphic paleontology in the early 19th century. Some great scientists, Charles Lyell in particular, denied direction altogether because they viewed the earth as a system in dynamic steady state throughout its recorded geological history (*1*). At the other extreme, many devotees of direction have sunk their rationale so deeply in compelling biases of personal psychology or surrounding culture—from the optimism of steady progress toward human consciousness to the pessimism of *Götterdämmerung* in the frozen, entropic wasteland of an exhausted sun—that their selective presentation of evidence commands little respect. The tailoring of ambiguous data to a priori hope has been so customary and pervasive that the subject of direction in life's history has hardly been addressed by modern paleobiology, despite its persistence as an ineluctable topic in popular literature (*2*).

Yet we believe, perhaps only as children of our culture, that scarcely any question can be as important as the issue of "vectorial properties" for the history of life. History, as usually understood, is not merely a string of unrepeated events, but a skein that unwinds in a definable way. The issue of direction must be rescued as a subject fit for rigorous study.

Physicists have maintained an interest in direction, if only (paradoxically) because so few of nature's laws specify a temporal vector of results. Eddington dubbed the second law of thermodynamics "time's arrow" because increasing entropy defines the major constraint that laws of physics and chemistry impose upon the unrolling of events in time (*3*). Richard Morris (*4*) could identify but four other arrows, all controversial or ill-defined: the expansion of the universe, irreversible decay of the neutral K meson into two particles, the travel of electromagnetic waves into the future, and the admittedly subjective arrow of psychological time.

When paleontologists have tried to identify vectors of time, they have usually invoked properties of life as an entirety. Thus, after a decade of intense debate, paleobiologists have reached an apparently stable consensus (*5*) that biases of the fossil record can be reliably factored out to detect a signal of increasing diversity for shallow water marine organisms during the Mesozoic and Cenozoic eras, perhaps following a long plateau of Paleozoic stability (*6*).

We wish to propose a more operational and testable approach to the search for vectors of life's history. Since evolution is, fundamentally, a genealogical process, why not study lineages rather than heterogeneous totalities? Why not search for statistical regularities among large samples of lineages, rather than for overall appearances in the single domain of life itself?

Consider Morris' (*4*) definition of an arrow of time—"we mean only that the world has a different appearance in one direction of time than it does in the other." Or, if you take life's actual tape and run it backward, would you know that the story could not happen this way? The arborescent topology of lineages, with new species arising by branching, imparts a clear arrow to evolutionary time—if lineages start to join into trunks, the tape is backward. Can an arrow of time be defined quantitatively, by portraying the history of lineages in the standard way as clade diversity diagrams (Fig. 1), a technique favored since the earliest days of stratigraphic paleontology (*7*). (A "clade," or segment of an evolutionary tree, derives from the Greek word for branch.) Each of these diagrams portrays a lineage or taxonomic group: the vertical axis represents time, the horizontal axis, diversity at any time (usually measured as number of coexisting taxa). The diagrams are conventionally drawn as symmetrical about their midline.

In this format, we pose an operational definition for arrows of time: does any asymmetry exist, statistically defined over large numbers of lineages, in the vertical dimension of clade diversity diagrams? If bottoms of lineages are definably different from tops, then evolutionary time has a direction, and the morphology of clade diversity diagrams can specify whether life's tape is running properly forward or illegitimately backward. We wish to replace the grand, but vague and noisome notion of progress with a question almost risibly limited by comparison—but imbued with the twin virtues of definition and testability: if you were handed a chart of clade diversity diagrams with unlabeled axes, would you know whether you were holding the chart upside down or right side up?

We write this article because each of us, independently in our studies of clade diversity diagrams at different levels and for diverse purposes, has discovered the same temporal asymmetry as a statistical property of groups of clades. We propose that this asymmetry—a signature of bottom heaviness expressed in several ways—may define a new arrow of time to specify the direction of evolution.

S. J. Gould is at the Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138. N. L. Gilinsky is in the Department of Geological Sciences, Virginia Polytechnic Institute, Blacksburg, VA 24061. R. Z. German is in the School of Dental Medicine, Washington University, St. Louis, MO 63130.

A Measure of Asymmetry

Any taxonomic group, if properly defined, originates as a single species, builds to maximum diversity (often in a complex pattern of fluctuation) and then (unless it be still extant) declines to extinction. The relative time of waxing and waning might provide a measure of temporal asymmetry. Clades may have their period of greatest diversity at the midpoint of their geological duration (no temporal asymmetry), nearer the beginning (producing a bottom-heavy clade), or nearer the end (a top-heavy clade). If clades are characteristically either top or bottom heavy, then life has an asymmetry that can serve as an arrow of time.

Both directions of asymmetry have been defended with insecure data and misplaced confidence in the domination of one evolutionary process over another (*8*). Clades have been proclaimed bottom heavy because adaptive radiation should follow evolutionary breakthrough, or top heavy because mass extinction so often cuts off a group at high diversity, thereby suppressing a period of gradual decline before extirpation. Rather than defend potential reasons, paleontologists should first ascertain whether either of these patterns is statistically dominant.

Beginning in 1973, Raup *et al.* (*9*) developed a random model to generate clade diversity diagrams as a null hypothesis for assessing the basis of order in the fossil record. For comparison with this model, they also began to develop a compendium of actual clade diversity diagrams, beginning at the lowest operational taxonomic level of genera within families—a project originated by Sepkoski and continued with remarkable and unexpected results (*10*).

As part of this program, Gould *et al.* (*11*) developed a set of clade statistics for the quantitative study of clade diversity diagrams. They included a simple measure of temporal asymmetry, *CG* or center of gravity.

Center of gravity is defined as the relative position in time of a clade's mean diversity, not as its time of maximum diversity (a transient moment of little significance). The simple calculation is most easily grasped by turning the clade diversity diagram on its side and treating the half above the midline as an ordinary histogram with time scaled from 0 to 1, and the mean calculated in the usual way as

$$CG = \frac{\sum_{i=1}^{n} N_i t_i}{\sum_{i=1}^{n} N_i}$$

with each class interval as a stage of geological time, and frequency in each interval as the number of taxa living at that time.

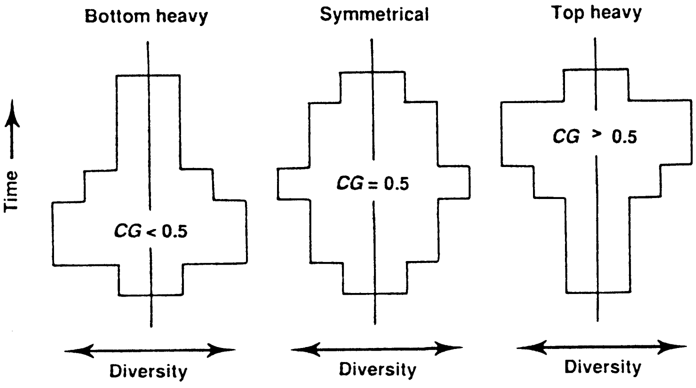

Fig. 1. Idealized clade diversity diagrams for bottom-heavy, symmetrical, and top-heavy clades.

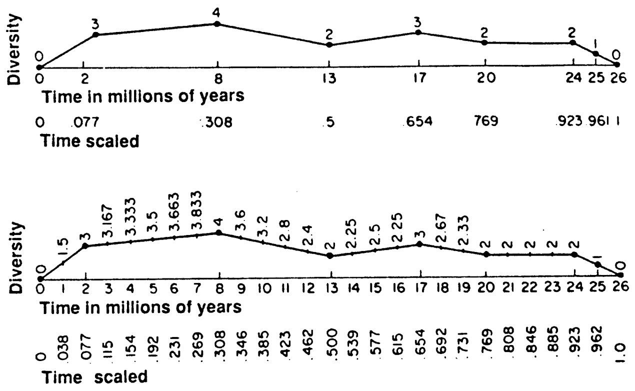

Fig. 2. Two modes of calculating *CG* as a response to the problem of unequal stage lengths. Top (method two of our text) considers each stage only once regardless of its length and yields $CG = 0.516$. Bottom (method three) interpolates a value for each million-year interval and yields $CG = 0.448$. We favor, and have generally used, uniform sampling schemes like method three.

In an obvious match with our intuitions (Fig. 1), clades with *CG* equal to 0.5 have their greatest weight at their midpoints, *CG* less than 0.5 defines bottom-heavy clades, and *CG* greater than 0.5 top-heavy clades. Mean *CG* is 0.5 in a random system treating all times and all lineages alike, and applying to each lineage an equal probability of branching or becoming extinct in each stage of time (*9*). Thus, in documenting an empirical pattern of *CG* less than 0.5 for real clades, we believe that we have identified a basic, nonrandom (and time-ordering) property of life's history.

Asymmetry by Time of Origin

Marine invertebrates. Gould *et al.* (*11*) calculated *CG* for 703 clades at the level of genera within families for eight major groups of marine invertebrates. We used only extinct clades in this analysis, since living clades have not yet run their course and can yield no prediction about the shape of evolutionary histories.

The stratigraphic distribution of *CG* reveals a marked asymmetry, with clades of $CG < 0.5$ concentrated early in the history of Metazoa, and no systematic departure from symmetrical $CG = 0.5$ for life's later history.

In Table 1, we divide the clades of each major group into two categories: those arising during the Cambrian and Ordovician periods and those originating later in geological time. The base of the Cambrian represents a crux in life's recorded history: the "Cambrian explosion" when nearly all basic designs of invertebrate life enter the fossil record for the first time. Without exception, for each of eight groups, mean *CG* for a large sample of Cambro-Ordovician clades is less than mean *CG* for clades of later origin. Moreover, mean *CG* for the total sample of 350 later clades is as close to the symmetrical 0.5 of random models as anyone could expect (0.4993), whereas 353 Cambro-Ordovician clades show a significant tendency to bottom heaviness at $CG = 0.482$.

Therefore, early arising clades of marine invertebrates have a characteristic bottom-heavy asymmetry (statistically defined in large samples), whereas clades arising later are temporally symmetrical. If presented with a complete chart of clades for marine invertebrates, we could orient the array in time by considering only the distribution of temporal asymmetry among clades.

Confirmation at another taxonomic level and with other modes of calculating CG. As a natural experiment, the fossil record has both strengths and weaknesses compared with usual laboratory standards—strengths in the amplitude of time provided, weaknesses in

Table 1. Values of CG for early and later arising clades. Clade sample sizes are shown in parentheses and designated as total: early arising, later arising. For Tertiary mammals (124:40, 84), CG values are 0.474 and 0.508 for the Paleocene and Eocene and later, respectively.

Clade	Cambrian-Ordovician	Silurian and later
Brachiopods (185:81, 104)	0.474	0.500
Graptolites (26:10, 16)*	0.460	0.508
Bivalves (87:17, 70)	0.500	0.510
Paleozoic corals (36:10, 26)	0.476	0.497
Archaeogastropods (58:24, 34)	0.481	0.498
Ostracods (68:32, 36)	0.471	0.485
Trilobites (138:124, 14)†	0.488	0.519
Nautiloids (105:55, 50)	0.485	0.487
Total (703:353, 350)	0.482	0.499

*Pre-Arenig versus Arenig and later. †Pre–Middle Ordovician versus later.

the poor controls, often with marked nonrandom biases (*12*). Even a procedure so apparently unambiguous as the calculation of CG must be carefully scrutinized. Consider, for example, the effect of inhomogeneity of time intervals.

A properly controlled experiment would devise equal time intervals for the measurement of frequencies, but the geological time scale, developed before the advent of radiometric dating, and based on the peculiarities of faunal history, is not measured in even increments. The 77 stages that we used to calculate CG (*11*) are not alike in length; more seriously, their disparity has a marked temporal bias since Paleozoic stages are longer on average than Mesozoic and Cenozoic stages (10.36 million compared with 5.49 million years).

The effect of decreasing stage length on CG depends on mode of calculation. If, as in the previous section (*11*), we calculate a contribution for each group in each million-year interval, we may overrepresent the "weight" of long intervals by dividing them into more units of a million years each. If, on the other hand, we count each stage only once at the midpoint of its actual age, then we risk the opposite bias of putting too much weight on more closely spaced samples (see Fig. 2).

This bias of directional decrease in stage length does not affect our previous calculations for clades of genera in families because so few clades pass through the great Permian extinction (when up to 96 percent of species died) (*13*). Nearly all clades at this level are either exclusively Paleozoic, or exclusively Mesozoic-Cenozoic. No directional biases exist for stage length within either of these two intervals. Spearman's rank correlation for stage length versus temporal order is insignificantly different from zero within each interval (0.012 for the Paleozoic, 0.258 for later times). For our key comparison of Cambro-Ordovician with later Paleozoic stages, mean durations are nearly the same (10.58 million versus 10.24 million years).

We did have to consider this bias when we tested the generality of our previous result at the higher taxonomic level of families within orders (where several clades cross the Permian boundary). To test for robustness of conclusion with different methods of calculation, we devised three disparate techniques to treat the problem of varying stage lengths for the 59 extinct, "well skeletonized" clades of families within orders from Sepkoski's compendium (*10*).

We calculated CG in three different ways: (i) by treating all stages as equal in length; (ii) by entering the diversity for each stage only once regardless of its length and considering each stage at the midpoint of its actual time according to Eq. 1, a procedure that overemphasizes short intervals; and (iii) by our favored and least biased method of calculating at each million-year interval and interpolating values between actual data points as in Fig. 2.

All three techniques yield a statistically significant positive slope, indicating greater bottom heaviness of clades that arise early in time (Fig. 3). For the three techniques, F tests for the probability of zero slope yielded $P = 0.0038$, $P = 0.0161$, and $P = 0.0124$.

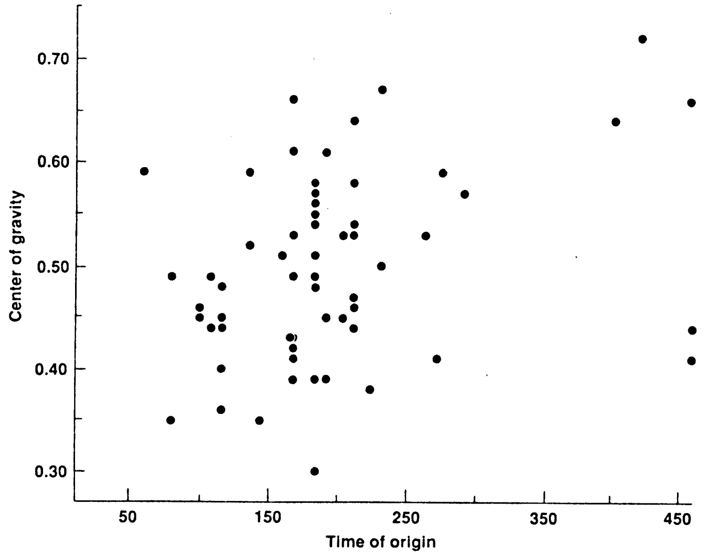

Fig. 3. Center of gravity as a function of time of origin from the base of the Vendian for extinct clades of families within higher taxa, calculated by the uniform sampling scheme of method three.

Confirmation for another group and environment. Since shallow water marine invertebrates dominate the fossil record, the robustness of bottom-heavy asymmetry in early arising clades (over two taxonomic levels and several modes for calculating CG) does identify a basic signature of life's history. Still, we must ask whether this correlation of $CG < 0.5$ with early origin represents a general phenomenon or only a historically contingent fact of invertebrate radiation in the sea.

Gould *et al.* (*11*) argued for generality by considering another group in another place: mammals in terrestrial environments. They calculated CG for clades of the Tertiary flowering of mammals following the late Cretaceous extinction of dinosaurs, dividing the sample by time of origin into 40 early arising Paleocene clades and 84 clades of Eocene and later appearance. They found the same pattern of bottom-heavy asymmetry for early clades ($CG = 0.474$) and symmetry for later clades ($CG = 0.508$).

German (*14*) then compiled more complete data for the 2180 genera with stratigraphic resolution to geological stage (*15*). These genera form clades for 256 families; of these, 165 are extinct, and therefore suitable for this analysis.

Figure 4 shows a plot of mean CG as a function of time of origin

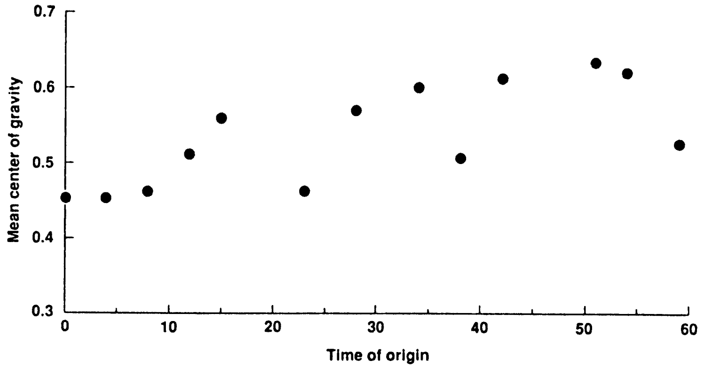

Fig. 4. Average CG for clades originating in each Tertiary stage as a function of time of origin since the base of the Tertiary for mammalian clades of genera within families.

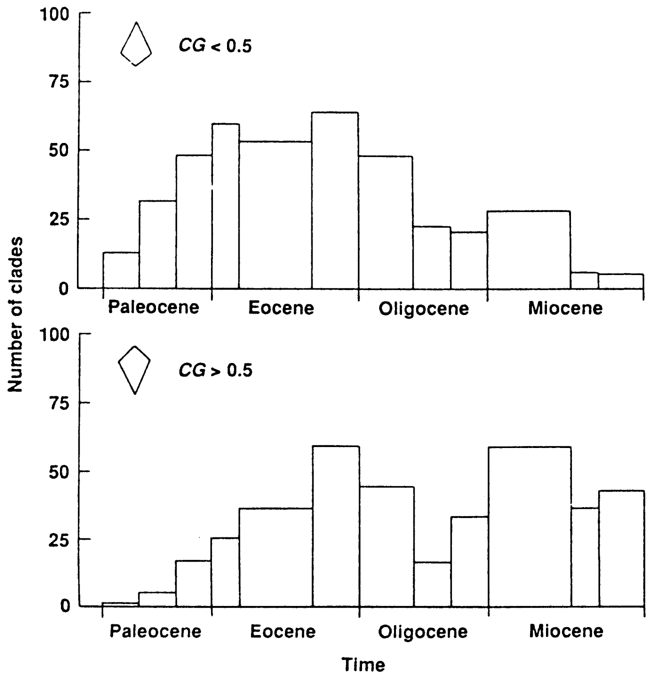

Fig. 5. Histograms for top-heavy and bottom-heavy clades of mammals (genera within families) at each stage of the Tertiary.

for extinct clades. Spearman's rank correlation for *CG* versus temporal order is a statistically significant 0.692 ($n = 13$). Clades that originate during the three Paleocene stages have mean $CG = 0.455$; for clades arising during later stages, $CG = 0.559$. Biases of unequal stage duration do not affect this division because the two segments do not differ, with Paleocene stages averaging 4.0 million years in length, and later stages 4.9 million years. Figure 5 shows histograms for numbers of bottom- and top-heavy clades present at each stage. Total number of clades rises as mammals diversify, then falls as fewer and fewer extinct clades occupy more recent faunas; but note how the proportion of bottom-heavy clades begins at a maximum and falls steadily through the Tertiary, being first surpassed by top-heavy clades in the late Oligocene.

Caveats

The tabulated clades of this and other studies in the same tradition view the actual history of life through a glass darkly for two basic reasons. First, imperfections in the fossil record guarantee that observed patterns are a biased sample of what actually happened. Precise quantitative corrections can rarely be made, and if actual results lie in the same direction as demonstrated biases, secure interpretation may be impossible. In practice, we attain greatest confidence when results are contrary to a primary bias. Since quality of preservation and quantity of available sediment increase as we approach the present (*12*), the known fossil record must impose a strong artifact favoring top-heavy clades. Since we have found an actual asymmetry of bottom-heaviness—and in the oldest clades at that—we feel confident that we have detected a real pattern (weakened if anything by biases of the fossil record).

The second reason—convention in taxonomic practice—is often harder to assess, and more of a dilemma in this study. We have spoken of clades throughout this work as though they represent true branches on life's tree. In fact, our clades are defined as established taxonomic groups. Since taxonomy is supposed to record evolutionary relationship, this difference between operational and conceptual definitions should not matter. However, a disparity between traditional systematic practice and strict genealogical criteria indicates that our taxonomic definition of clades may pose problems.

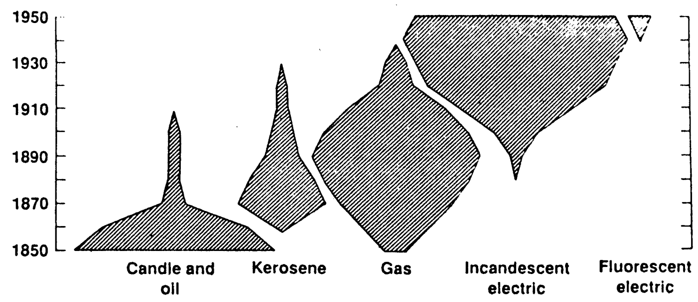

Fig. 6. Clades for the waxing and waning of lighting devices used in Pennsylvania. Data (*22*) are in percentages.

Properly defined clades are monophyletic in the broad sense of tracing ancestry to a single species. Many, however, are not monophyletic in the strict sense because they exclude some descendants branching off within the clade's history but becoming so divergent that taxonomists designate them as a separate group (birds become an independent class and are not retained within the Dinosauria, for example). Clades that exclude some descendants of their ancestral species are called paraphyletic—and many traditional taxonomic groups fall into this category. Paraphyly may raise a particular problem for this study because it may impose the type of bias that we strive to avoid—one that favors results consistent with our hypothesis (*16*). For paraphyletic clades may tend to be bottom heavy because some later arising descendants are excluded by incorporation into new groups.

We offer three responses to this objection. First, many systematists defend the validity of paraphyletic groups as striking a proper balance between genealogical and functional bases of evolutionary similarity (*17*). If we seek such a balance, then we should be using traditional groups, paraphyly and all—though we do acknowledge the strong arguments for the strictly genealogical alternative of cladistic arrangement (*18*).

Second, our particular results are probably not much affected by the problem of paraphyly. We find bottom heaviness only for early clades, but paraphyly is a consequence of rapid divergence within a sublineage, and such accelerations of rate occur throughout life's history; we would be more concerned about this bias if we had detected a time-independent signal of bottom heaviness.

Third and finally, the bottom-heavy character of old clades at the highest taxonomic levels not only supports our pattern, but also indicates that our documented temporal asymmetry may display a fractal character of self-similarity at all scales. These markedly bottom-heavy highest level clades range from the phylum Echinodermata, with its massive radiation of early Paleozoic classes and later stabilization of a few survivors (*19*), to the clade of the entire coelomate Metazoa, where one Cambrian quarry in British Columbia, the famous Burgess Shale (*20*), contains more diversity of anatomical design than all living members combined. These clades of largest scale are strictly monophyletic [unless Jefferies' decidedly heterodox derivation of vertebrates from carpoid echinoderms be sustained (*21*)].

In any case, we cannot solve this problem by verbal argument. We have presented the clade diversity diagrams for groups now recognized in our standard taxonomies. The bias of paraphyly can only be tested by running a similar analysis upon clades defined by criteria of strict genealogy and monophyly. We hope that such a complete and fully cladistic taxonomy will soon be published so that we or others may make such a test.

Conclusions and Prospects

The usual interpretation attributes our pattern of early bottom heaviness to "adaptive radiation" following either an evolutionary innovation or an ecological vacuum caused by extinction of a previously dominant group. (Our two cases of Metazoa and mammals represent the first filling of life's ecological "barrel" for multicellular animals, and the radiation of mammals into roles formerly occupied by dinosaurs.) In more general terms, bottom-heavy asymmetry arises when an initial emptiness permits unusual opportunity for diversification (we reject the conventional designation, with no evidence beyond the rapid increase itself, of such radiations as "adaptive," because these are the very situations that may permit at least a short reign for drastic suboptimality). Clades diversify rapidly in ephemeral times of unusual opportunity and peter out in a world at or closer to equilibrium.

As a study of temporal pattern, evolution shares common ground with other sciences that treat historical connection as their primary source of order. The search for temporal asymmetry as a sign of direction might become a general pursuit in these disciplines, and methods developed in one field might be employed in others.

Clade diversity diagrams are used in other fields, though different terms and traditions have prevented the general appreciation of a fruitful isomorphism. Under the framework of "seriation," and with such colorful names as "battleship shaped curves," these diagrams have been used in archeology ever since the preeminent Egyptologist Sir Flinders Petrie excavated the great pyramid of Giza during the late 19th century. This early work often pursued a "backward" methodology, with dubious results. The "correct" shape of a clade diversity diagram (say, for a form of potsherd) was assumed a priori (the idealized, single waxing and waning of a "battleship shape"), and a temporal sequence was then constructed as the ordering of samples that best approximated this preferred shape. In more recent work, archeologists have usually followed the stratigrapher's credo that temporal order must first be known [see the elegant work of Deetz and Dethlefsen (*22*) on seriation of headstone designs in New England graveyards; the advantages of such objects for fine-scale temporal resolution can scarcely be overstated]. Figure 6 on the seriation of lighting devices in Pennsylvania (*23*) provides another example of temporally ordered percentages.

According to most evolutionists, natural selection drives the evolutionary change that produces clade diversity diagrams for life's history. Yet we surely do not exhaust the scientific content of patterns and asymmetries in these diagrams by invoking any particular efficient cause of change—lest the similarities of form across disciplines with different objects and mechanisms be reduced to the anecdotal or analogical.

Deeper principles of structural organization must regulate and constrain the shape of genealogical systems in time. Natural selection may generate the changes that fit these molds in natural history; some other process may serve the same causal role in archeology. But the structural principles that fashion the molds and set the constraints upon pathways of change may be more abstract, and therefore common to a broad range of disciplines wedded to differing immediate mechanisms.

Our documentation of the bottom-heavy asymmetry of life's clades, for example, may form part of a larger and more general study of innovation. We may be seeing the rapid expansion following breakthrough, and often missing the long thin tail that sometimes (or usually) precedes a burst to success, and that records the boundaries protecting stable systems against invasion by what may be superior innovations. Principles of incumbency and critical mass may explain the durability of inferior politicians, the delayed acceptance of efficient inventions (particularly if they impose a ramifying restructure upon many surrounding institutions), and the rapid hegemony of mammals only after they had passed nearly two-thirds of their geological existence as small creatures in the interstices of a dinosaur's world. We all recognize these principles as woolly and poorly structured verbalisms; perhaps the quantitative study of asymmetry in clade diversity diagrams might suggest a pathway to a more fruitful and unified treatment over a wide range of disciplines.

No individual molecule can illustrate the thermodynamic law of entropy; but large populations give an unerring direction to time. No single clade can record the direction of evolutionary time by its asymmetry, but the statistical properties of clade diversity diagrams may identify life's arrow. The shape of what has been may tell us about the shape of things to come, or even about the temporal forms of organization itself.

REFERENCES AND NOTES

1. On this crucial substantive meaning of Lyell's complex "uniformitarianism," see R. Hooykaas [*The Principle of Uniformity* (Brill, Leiden, 1963)], M. J. S. Rudwick [*The Meaning of Fossils* (Macdonald, London, 1972)], and S. J. Gould [*Time's Arrow, Time's Cycle* (Harvard Univ. Press, Cambridge, MA, 1987)].
2. The chief architects of the modern synthesis of evolutionary theory have focused these popular works (but very little technical effort) upon the issue of progress [G. G. Simpson, *The Meaning of Evolution* (Yale Univ. Press, New Haven, 1949); J. Huxley, *Evolution in Action* (Chatto & Windus, London, 1953); Th. Dobzhansky, *The Biology of Ultimate Concern* (New American Library, New York, 1967)].
3. H. F. Blum, *Time's Arrow and Evolution* (Princeton Univ. Press, Princeton, NJ, 1951).
4. R. Morris, *Time's Arrows* (Simon & Schuster, New York, 1984).
5. J. J. Sepkoski, Jr., R. K. Bambach, D. M. Raup, J. W. Valentine, *Nature (London)* **293**, 435 (1981).
6. This increase may be a contingent result of continental breakup and dispersion, rather than an intrinsic and predictable outcome of evolutionary theory. Such contingent vectors are easily reversible and do not rank as stable arrows of time.
7. So far as we know, Agassiz's pre-evolutionary account of fossil fishes represents the earliest attempt to portray the entire history of a group as a set of clade diversity diagrams [L. Agassiz, *Les poissons fossiles* (Neuchâtel 1833–1843), vol. 1, p. 170].
8. The small literature on quantification of clade diversity diagrams begins with John Phillips' classic *Life on the Earth* [(Macmillan, London, 1860)] and has been pursued most assiduously in our time by the leading East German paleontologist A. H. Müller [*Grossabläufe der Stammesgeschichte* (Fischer, Jena, 1961)].
9. D. M. Raup, S. J. Gould, T. J. M. Schopf, D. S. Simberloff, *J. Geol.* **81**, 525 (1973); D. M. Raup and S. J. Gould, *Syst. Zool.* **23**, 305 (1974).
10. J. J. Sepkoski, Jr., *Milwaukee Public Mus. Contrib. Biol. Geol.* **51**, 1 (1982); J. J. Sepkoski, Jr., *Paleobiology* **10**, 246 (1984); J. J. Sepkoski, Jr., and D. M. Raup, in *Dynamics of Extinction*, D. Elliot, Ed. (Wiley, New York, 1987), pp. 3–36.
11. See S. J. Gould, D. M. Raup, J. J. Sepkoski, Jr., T. J. M. Schopf, and D. S. Simberloff [*Paleobiology* **3**, 23 (1977)], for details of sources used to compile clades, definition of geological stages, and calculation of clade statistics.
12. D. M. Raup, *Bull. Carnegie Mus. Nat. Hist.* **13**, 85 (1979); P. W. Signor III, *Geology* **10**, 625 (1982); G. Retallack, *Paleobiology* **10**, 59 (1984).
13. D. M. Raup, *Science* **206**, 217 (1979).
14. R. Z. German, thesis, Harvard University, Cambridge, MA (1983).
15. Data from A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966).
16. D. M. Raup (personal communication) impressed the importance of this argument upon us.
17. E. Mayr, *Zeitsch. Zool. Syst. Evol. Forsch.* **12**, 94 (1974).
18. N. Eldredge and J. Cracraft, *Phylogenetic Patterns and the Evolutionary Process* (Columbia Univ. Press, New York, 1980).
19. J. Sprinkle, in *Echinoderms*, T. W. Broadhead and J. A. Waters, Eds. (Department of Geological Sciences, University of Tennessee, Knoxville, 1980), pp. 15–26 and 86–92; J. Sprinkle in *Echinoderm Studies*, M. Jangoux and J. M. Lawrence, Eds. (Balkema, Rotterdam, 1983), pp. 1–18.
20. H. B. Whittington, *The Burgess Shale* (Yale Univ. Press, New Haven, 1985); S. Conway Morris, *Palaeontology* **29**, 423 (1986).
21. R. P. S. Jefferies, *The Ancestry of the Vertebrates* (British Museum of Natural History, London, 1986).
22. J. A. Deetz and E. Dethlefsen, *Southwest J. Anthropol.* **21**, 196 (1965); E. Dethlefsen and J. A. Deetz, *Am. Antiq.* **31**, 502 (1966).
23. J. A. Ford, *A Quantitative Method for Deriving Cultural Chronology* (Pan American Union, Washington, DC, 1962).