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The promise of paleobiology as a nomothetic, evolutionary discipline[1]

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Abstract.—During the past 20 years, paleobiology has established the foundations of a nomothetic science based upon evolutionary theory. This radical break with a past philosophy based on irreducible historical uniqueness is still impeded by (1) overreliance upon the inductivist methodology that embodied this previous philosophy, and (2) an unadventurous approach to biology that attempts passively to transfer the orthodoxies of microevolutionary theory across vast stretches of time and several levels of a hierarchy into the domain of macroevolution. I analyze the major trends of recent invertebrate paleobiology in the light of these two impediments. The formulation, by paleobiologists and with paleobiological data, of new macroevolutionary theories should end the subservience of passive transfer and contribute, in turn, to the formulation of a new, general theory of evolution that recognizes hierarchy and permits a set of unifying principles to work differently at various levels.

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I. A Great Instauration? A Roaring Mouse? Or Something Between?

Of the psychology of his time, William James complained bitterly in 1892. It was, he argued, no science at all despite its pretenses, but only "a string of raw facts; a little gossip and wrangle about opinions; a little classification and generalization on the mere descriptive level, . . . not a single proposition from which any consequence can causally be deduced. We don't even know the terms between which the elementary laws would obtain if we had them. This is no science, it is only the hope of a science." Charles Spearman, the man who brought multivariate quantification to psychology by inventing a rudimentary form of factor analysis in 1904, thought little better of his profession 45 years later, calling it a "Cinderella among the sciences" (1937, p. 21) for the same reasons that had motivated James' lamentation: domination of the profession by a methodology of mindless empiricism leading to no generalities worthy of the name "law."

Until recently, paleontology suffered from a similar reputation, largely deserved. In 1969, the editors of *Nature* even used the very name of the profession as a derogatory synecdoche for sciences that seek no synthesis and fractionate into tiny groups of experts on the less and less: "Scientists in general might be excused for assuming that most geologists are palaeontologists and most palaeontologists have staked out a square mile as their life's work. A revamping of the geologist's image is badly needed" (Anonymous 1969, p. 903). But our profession now wears the glass slipper and, if not queen of the evolutionary ball, at least cuts a figure worth more than a passing glance.

In this work, I propose to examine how this change arose and, more importantly, what still impedes its larger promise. This paper is not a review article; it is a partisan statement. I claim, in brief, that this new wave of excitement (if not the "great instauration" of which Francis Bacon spoke) arises from the incorporation into paleontology of a synthetic, workable and expansive evolutionary perspective. If I may invoke Spearman's Grimm metaphor just one more time, Simpson played the prince in 1944 with the publication of *Tempo and Mode in Evolution,* but his shoe did not fit comfortably for another 20 years or so. In fact, I believe that paleontology has had a cyclic history for the generation of excitement, and that the peaks

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[1] This article (in two parts) is one of four requested on the topic "Status of Paleontology—1980." The other three (on microfossils, paleobotany and vertebrate paleontology) were delayed and will appear in subsequent issues.

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can all be correlated with the infusion of biological concepts (our field did not always rest in the doldrums described so graphically by *Nature's* editors). Previous episodes of biological excitement have included: 1) the heady days of Cuvier's time when the greatest minds of Europe took up paleontology and the facts of extinction and succession of faunas were established; 2) the early days of evolutionary thought when paleontologists sought (ultimately without success) a general non-Darwinian theory based on neo-Lamarckian ideas and the theory of recapitulation (as in the work of E. D. Cope and Alpheus Hyatt); 3) German paleobiology of the 1920's, inspired by Dollo's functional approach, but extinguished in its promising youth by Hitler's rise, both from without and from within (Abel joined the Austrian Nazis).

But amidst all this movement, I still sense a strong inertia and potential limit. I do not believe that the limit is primarily one of fact—the traditional, and lamentably accurate, argument about the poverty of the fossil record. About this we can do little beyond learning to assess its influence (quantitatively, if possible—Raup 1978; Signor 1978) and striving for novel methods to wrest information from a reluctant earth. I believe, instead, that the limit arises largely for two reasons reflecting an inadequacy of innovation in theory and ideas: 1) restrictive methodology—in fact, the one that James lamented—still controlling much of our work, and 2) an approach to biology that condemns us to imitation and exemplification, rather than encouraging novelty.

Many historians have commented that the most curiously revealing statement in Darwin's autobiography comes close to being an unconscious lie—his claim that he "worked on true Baconian principles, and without any theory collected facts on a wholesale scale." For Darwin did no such thing. He tested theories from the start and abandoned several of them before fixing on one that he derived by creative transference from such disparate sources as the Scottish economists, the French positivist Comte, the Belgian statistician Quetelet, and the grimly conservative parson Malthus, leavened by some turtles, toxodonts, birds and five years of contrary argument from the devout Captain FitzRoy (Schweber 1977). Yet so great was the prestige of strict inductionism as a philosophy of science that, in writing this moral homily for his children (Darwin did not intend his autobiography for publication), one of the most creative and least inductive of men restructured himself to fit a norm that never did exist.

This norm of inductivism holds that science begins with pure facts and works its way up to synthesis, integration and theory (if it ever gets there at all) by collecting, collating and arranging these hard bits of unsullied information. Philosophers and historians have shown *ad nauseam* that this idyll bears little relation to creative science as actually pursued. Its fallacies are primarily two: First, facts do not come to us as objective items seen in the same unambiguous way by all reasonable people. Theory, habit, prejudice and culture all influence the facts we choose to observe and the way in which we perceive them. Second, the construction of theories is not a "second story" operation in science, an activity to be pursued after constructing a factual ground floor. Theory informs any good scientific work from the very beginning; for we ask questions in its light, and science is inquiry, not mindless collection. Moreover, the sources of theory are manifold; new ideas arise more often by the creative juxtaposition of concepts from other disciplines (as in Darwin's case) than from the gathering of new information within an accepted framework.

I think that few scientists would now disagree with these claims (though they would have shocked many paleontologists of previous generations). But agreement in the abstract is such a different phenomenon from incorporation into the guts of practice. I believe that many of us work in dissonance. We can mouth Kuhnian modernisms about the role of theory, but we remain inductivists in our heart of hearts.

It shouldn't be necessary to say so, but I do want to assert that this perspective on the relationship of fact and theory does not, in any way, demote the importance of facts. Any demotion would be perverse in a field that is probably unrivalled for the sheer fascination of its phenomenology. (What other profession can win a front page story in the New York Times for finding a big object just a little larger than any discovered before—the scapula of a brachiosaur in this case?) I only advocate a different role for facts, one that would make them an intrinsic part of the process of discovery, not just a miscellaneous collection of what we happen to encounter.

All perspectives can be vulgarized. Einstein had to live with the claim that he meant to say "all is relative." Marx eventually denied that he was a marxist. Darwin's subtle vision of natural selection has often been perverted to a rigid statement that every bump on every bone is a direct adaptation and that we truly live in the best of all possible worlds. The perspective that I present, now a common property of so many historians, philosophers and scientists, has been misunderstood and trivialized as an argument that facts are of secondary importance in science or, even worse, that there is no such thing as truth, but only cultural prejudice. We need a partnership of facts and ideas. Kant was advocating a marriage between equal partners, not making a sneaky judgment of relative value when he quipped that percepts without concepts are blind, but that concepts without percepts are empty.

The marriage cannot occur yet in paleontology, because one partner still dominates, though the other advances apace. Three primary reasons—one good, one historical, and one indefensible—underline the persistent hold of inductivism upon paleontological practice:

i) Paleontology is, in large part, a historical discipline charged with documenting the irreversible and unrepeatable events of life's history. In such fields, pure fact has a legitimate and intrinsic value that it does not possess in other disciplines. We care very much that *Neotrigonia* lacks (except in its larval shell) the discrepant ornament that characterizes most Mesozoic trigonians. The splinter that retarded the ball rolling down this particular inclined plane is merely a nuisance.

ii) Invertebrate paleontology has cast its institutional allegiance with geology—more by historical accident than by current logic. When it operates as a geological discipline, paleontology has tended to be an empirical tool for stratigraphic ordering and environmental reconstruction. As a service industry, its practitioners have been schooled as minutely detailed, but restricted experts in the niceties of taxonomy for particular groups in particular times. We may affirm the absolute necessity of comprehensive geological training for success in paleontology, but also admit that strictly non-biological approaches have not infused our profession with the excitement of ideas. To particularize Kant's dictum: with all biology and no geology, paleontology is empty; but with geology alone, it is blind.

iii) Inertia, pure and simple. It is easier to continue in an old way; reform of ideas is much cheaper and easier than alteration of practice.

Inertia also underlies my second complaint about insufficient innovation. If a persistent inductivist methodology marks part of our failure, then a tendency to be uninnovative when we do break through inductivist shackles characterizes the other part. When we do use our data to explore questions in evolutionary theory, we tend to choose our questions by passive transference from microevolutionary studies. We take the evolutionary concepts formulated for us by students of modern populations and we try to show that ancient ones lived by the same rules. But where does this lead beyond exemplification based on imperfect data? Surely no one doubts this aspect of uniformity. Such a passive procedure merely binds us to a different kind of subservience. We become vassals to a theory developed elsewhere and we wait for the crumbs (or plums) that power our applications. It may be a nobler form of serfdom than the thrall of thoughtless gathering, but independence it isn't.

A general theory of paleontology can only emerge from its status as guardian of the record for vast times and effects. If every evolutionary principle can be seen in a *Drosophila* bottle or in the small and immediate adjustment of local populations on the *Biston betularia* model, then paleontology may have nothing to offer biology beyond exciting documentation. But if evolution works on a hierarchy of levels (as it does), and if emerging theories of macroevolution have an independent status within evolutionary theory (as they do), then paleontology may become an equal partner among the evolutionary disciplines.

It may seem uncharitable to raise these points just when paleobiology is making so many promising steps in exactly the directions I advocate—and especially in a journal that serves as the locus for most of them. But I reside in that most dangerous of states—a positive feedback loop. The promising steps merely whet my appetite; there is so much more to be done.

Thus, in the four remaining parts of this work I explore the two impediments—inductivism as a methodology and passive transfer as a biological approach—in more detail, discuss the major trends of current paleobiological work in their light, and express some hopes for the immediate future. Then, in the shorter companion piece, I ask if a new, general theory of evolution is emerging. My tentative yes does not merely presage (I hope) a new body of information for passive transfer—for the new theory, by acknowledging hierarchy as fundamental, not only affirms a bounded independence for macroevolution but also owes some of its origin to the data of paleobiology.

II. The Method of Paleobiology

One might argue that frequent self-examination is a sign either of under-confidence or of insufficient impetus to move a field forward by the strength of its own technical advances. One might also argue that it represents measured and intelligent introspection, citing Montaigne's inscription for his library: "I do not understand; I pause; I examine." In any case, invertebrate paleontology has been producing multi-authored self-examinations at the rate of about one a decade of late.

The last two, Kummel's 1954 tabulation and Moore's 1968 compendium, proceed in the classical tradition of inductivist methodology: group by taxonomic group. Moore's, for example, begins with 6 general topics, none on evolution (zonation and correlation, techniques, biometry, paleoecology, paleogeography and paleomagnetism, Precambrian fossils), continues with 7 essays on geographical areas, defined politically, and concludes with 36 essays on groups. Not an explicit recognition of evolution among 50 topics—except in the old inductivist sense that equates evolution with descriptive phylogeny (an unfortunate usage perpetuated today by many paleontologists). Opinions vary, but I cannot read either of these documents without a pervasive feeling that this profession knows a great deal and gets excited about frightfully little of it. Moore explicitly declined to sum up and offered only this as a generalization (1968, p. 1377): "Paleontology today is in good hands . . . . The coming half century will witness appreciably more important and exciting advances in knowledge about past life on the earth than can be recorded here for the similar period now brought to a close."

All good scholars know that the way a discipline chooses to define its subfields both reflects its intellectual attitudes and, more importantly, channels thought and effort in particular directions. Thus, they will fight with dogged passion about subjects of definition that strike outsiders as minor semantic quarrels (e.g. Thurstone, 1924, on the definition of intelligence and the categories of psychology). As long as paleontologists define themselves primarily by favored taxa and times, we will not have a strong science based on evolutionary theory. For this definition reflects the inductivist belief that all good science begins in factual documentation and reaches theory only by an arduous process of gathering, collating, sifting, and ordering. In a profession so replete with facts, one can only stake out a limited range, mine it with industry, eschew generality, and hope for synthesis in the glow of maturity.

Simpson's *Tempo and Mode in Evolution* (1944) broke sharply with this tradition. Nothing proceeds in chronological sequence and only one of 36 figures portrays an animal (only two lower teeth of *Phenacodus* to be precise, and cribbed from Osborn at that). The other figures are pictorial models and graphs. The subject is evolutionary theory and the book tries to test a specific hypothesis—that the principles of modern genetics can encompass all events at whatever scale in the fossil record, and that the history of life offers no impediment to hopes for a unified theory of evolutionary processes.

Simpson's style of science has finally taken root in paleobiology. *Models in Paleobiology* (Schopf 1972) was purposely constructed as an exemplification of it. This journal is its conscious embodiment. (In the first two issues for 1979, graphs and pictorial models outnumber animals by 48 to 27. I myself would be happier with a more equal balance.) Paleontologists are now using facts to test ideas, or sometimes—and let's be honest—unconsciously selecting and manipulating facts to advance ideas. [All good movements have their flip side. Empiricism at its best awes us with sheer fascination and, at its worst, buries us in thickets of ephemeral systematics that must be completely reworked after the next wave of changing procedure. At its best, the testing of ideas jolts an accepted view and introduces fresh perspective to an old issue (could the Cambrian explosion really have no Cambrian cause and arise as the log phase of a sigmoidal process initiated earlier?—Sepkoski, 1978; why does within-habitat diversity reach a higher plateau in the Tertiary than before?—Bambach, 1977). At its worst, it becomes a domain for selective misrepresentation.]

Many traditional paleontologists have reacted to this new style with disdain and dismay. Some even fear that the science may wither as fewer and fewer facts enter the ground story. Certain important intersections of groups and times, I am told, now boast not a single specialist. In one sense, this fear is groundless outside the inductivist perspective that engenders it. If ideas arise only from facts and the facts stop flowing, then everything stops, and the science dies. But if ideas and facts are partners of potentially independent origin, then uneven representation of one side does not scuttle the enterprise (though a permanent undervaluing of either will lead to one or the other horn of Kant's dilemma). After all, paleontology survived for many years in a virtual void of ideas.

In another sense, this fear deserves our attention and respect. The asymmetry of fact and theory dictates that science without the second may be dull; but without the first, it is garbage. Facts needn't cover all areas like a seamless blanket, but their general absence guarantees sterility.

I can't imagine why any paleontologist would shun the opportunity for developing an area of empirical expertise. We have, first of all, the historical lesson that all great theorists in paleontology have been outstanding empiricists as well. Can you imagine Schindewolf without ammonites, Simpson without Mesozoic mammals, or Cuvier without his ibises and pachyderms. But, more importantly, and I don't know how else to say it, fossils are beautiful. Why would any sane person enter a field based upon them, and then operate only with abstractions?

Yet, in a third sense, the entire issue is false; for it rests on a confusion between levels—empirics itself and the methodology traditionally associated with it. Gregory Bateson, in his last book (1979), argues that many of our most acrimonious debates arise from "errors of logical typing"—particularly the confusion of individuals for classes or things for categories. Lamarck, for example, argued that environments affected the heredity of individuals. His version of transferring information between environments and organisms was correct, but he emphasized the individual rather than the population, and therefore missed the right level of transfer by one: "environment does have direct impact upon the gene pool of the population" (Bateson 1979, p. 118). No sensible modeller or tester of biological ideas has any quarrel with the copious gathering of data. If the entire field were engulfed by these newer procedures (a disaster to be avoided in our diverse world), data would not be devalued and its accumulation would continue apace, though with different motives. My complaint is with the next level of abstraction—not the data, but the methodology that enshrines its mindless collection as the basis of all proper paleontology.

I have argued so far that Simpson's procedure of modelling and testing has finally taken root and that it offers no challenge to the importance of facts. Nonetheless, its roots are still shallow, and much "explanatory" work in paleobiology proceeds in the old way under the inductivist credo. In the inductivist tradition, generalities must emerge from cases. The process is laborious and only leads to statistical regularities. Most traditional "laws" of paleontology—Cope's law of size increase, Williston's of reduction and specialization of serially homologous parts—are of this form, and usually lead nowhere. They represent, in James' lamentation, "a little classification and generalization on the mere descriptive level." (A very few classical generalities were formulated in James' preferred way—"propositions from which consequences can causally be deduced." Dollo deduced the law of irreversibility from principles of probability; it is a profound concept that captures the essence of complex science as historically contingent, yet causally constrained—Gould, 1970b).

Much paleobiological work continues in the "empirical law" tradition—it accumulates cases in the hope that some useful generality will emerge. I strongly suspect that such work, though intrinsically valuable for its elucidation of cases, will furnish no new or expansive generalizations. I would include here at least three important directions in modern paleobiology:

1. Community reconstruction. The reconstruction of communities sounds like the right thing to do. Isn't it the most integrative and general activity of all? Why divorce a taxon from its context (and study rates or patterns of lineages) when we might look at everything available and rebuild the dynamics of a community? But where does it all lead, and why is it being done? Suppose that we could proceed unambiguously, that we could enumerate taxa, determine relative abundances, assign trophic roles, and calculate biomass. At the end, we decide that ancient communities worked much like modern ones. Did we ever doubt it (and if we did doubt it, would this be the way to nurture suspicion)? Then we continue for other communities and find that they had familiar structure as well. (The procedure, of course, isn't even this favorable. Simplifying assumptions must be made, and they enter calculations with cascading effects upon final conclusions.) In the end, we have a series of reconstructions, but no general messages beyond an affirmation of uniformity that no one doubted.

Community reconstruction seems right because it represents the most comprehensive at-a-spot inductivism that we can attempt. It arises from the notion that gathering *all* the facts together will lead to induction of a bigger picture—as if the importance of generalities were a function of the number of facts used to generate them. But the picture is only, at best, a fact of higher order—a community instead of a brachiopod. The decision to extract and isolate—to study a particular lineage or a particular kind of interaction across communities—is not a surrender to nature's complexity. It represents, if done well, an intelligent selection of workable problems related to perplexing questions.

Community reconstruction will gain theoretical interest when it addresses unresolved biological questions, but not while it measures success by the fit of individual solutions to modern analogues, and proceeds by enumerating more and more individual solutions. Is there a vector of changing structure through time in similar physical circumstances? Do communities have a higher-order stability beyond the persistence of their individual species (see Olson's notion of chronofaunas—1962)? Do any patterns in the rise and fall of higher taxa result from the greater persistence of certain kinds of communities? What is the relationship, if any, between geological longevity and the stability of communities in ecological time? If the relationship be absent or oblique (as I suspect), then what does confer superior persistence upon a community?

2. Mechanistic functional morphology. The flowering of functional morphology has yielded a panoply of elegant individual examples and few principles beyond the unenlightening conclusion that animals work well. As particular studies of eminent utility in their own domain, these efforts have had great value—for we do need to know what this animal was doing in that place. But I think that higher hopes were once held (Rudwick 1964). I, at least, once harbored the naive belief that a simple enumeration of more and more cases would yield new principles for the study of form (Gould 1970a). But Newtonian procedures yield Newtonian answers, and who doubts that animals tend to be well designed? Interesting answers demand new questions, and empirical studies cast explicitly in their light. I suspect that functional morphology will fulfill its promise when it probes the situations in which animals are *not* well designed—developmental, phyletic, and architectural constraints as marks of history (Seilacher 1972; Gould and Lewontin 1979). As a key issue, I suggest: why is morphological space so sparsely populated, but so clumped where it is occupied? How much of clumping and non-occupation reflects good and untenable design (Raup 1966), how much the constraints of genealogy?

3. Biostatistics. No scientific vision is more intoxicating than the idea that one might manipulate an enormous matrix of objective data,

simplify it, and extract from its pattern an underlying causal structure. The history of statistics is strewn with such efforts, few successful. Factor analysis arose from the observation (Spearman 1904) that correlation matrices of mental tests rarely contained any but positive values (people who do well on verbal tests, tend to do well on arithmetic tests, etc.). Spearman extracted a first principal axis, called it G (for general intelligence), and assumed that he had identified a cerebral energy underlying all mental activity. But any nonrandom matrix must have a principal axis, and it needn't correspond to any physical reality. Positive correlation between mental tests may only embody a general effect conferred by good homes and education; it needn't capture an innate general intelligence.

Reams of data collected for no purpose and then submitted to statistical manipulation are rarely sources of new insight. Such a procedure represents inductivism at its worst—"if I can only get enough rigorously objective data, there must be something in it, or under it." Inductive statistics have their essential place in individual studies, but are rarely sources of new theory. They may, however, test new theory.

L. L. Thurstone, another pioneer of factor analysis in psychology, understood the role and limits of such statistical manipulation when he wrote (1935, p. xi): "No one would think of investigating the fundamental laws of classical mechanics by . . . factor methods . . . (But) if nothing were known about the law of falling bodies, it would be sensible to analyze, factorially, a great many attributes of objects that are dropped or thrown from an elevated point. It would then be discovered that one factor is heavily loaded with the time of fall and with the distance fallen but that this factor has a zero loading in the weight of the object. The usefulness of factor methods will be at the borderline of science." Newton's law, like all great generalizations, arose by ingenious conjecture, deduction of consequences, and testing in limited and controlled situations—not from the reduction of matrices gathered with no other purpose than an unformed desire to learn "something" about falling bodies.

Yet each of these three areas has also generated fruitful models and hypotheses. Consider three that may have been wrong or intractable: (1) The Bretsky-Lorenz (1970) hypothesis that communities stable in ecological time should contain species with reduced genetic variability and therefore be unstable under environmental shift in geological time. It attracted the attention of geneticists, underwent extensive testing (Gooch and Schopf 1973; Ayala et al. 1975), and failed. From this failure we learned more about community stability than all inductive reconstructions have supplied. (2) Rudwick's analysis of morphology by comparison with ideal "paradigms" or engineering optima (1961). It foundered on the difficulty of specifying function a priori (in order to know what paradigm to construct), but it clarified procedure and directed attention to the central problem of non-optimality. (3) Van Valen's law of stochastic extinction (1973), a hypothesis demanding statistical test by assessing deviations from linearity for curves formally similar to plots of radioactive decay. It may be wrong, or at least compromised (Raup 1975; Sepkoski 1975), but it jolted a profession to consider radical and stochastic alternatives to conventional wisdom. Science is, as Popper says, "conjecture and refutation." Utility and testability, not truth or falsity, are the criteria of fruitful models.

C. S. Peirce claimed that science advanced not by induction, but by "abduction"—literally by the creative grabbing and amalgamation of disparate concepts into bold ideas that could be formulated for testing. Paleobiology must follow this frustratingly bumpy and irregular—but ascending—path; for the smooth road of induction leads back upon itself.

III. What Shall Be Our Attitude Towards Biology

If we agree that the preferred method of paleobiology should be proposal and testing of ideas, then evolutionary biology must provide a primary pool for intelligent fishing. If my first complaint bemoaned a decision not to fish at all (the inductivist methodology), then my second frustration involves our characteristic manner of fishing when we choose to indulge—passively and unidirectionally, with no thought of stocking the pool in return.

Our primary stance towards evolutionary biology has been fundamentally uncreative: we have used our data to exemplify the principles of neontology, not to search for new principles or to think seriously about how existing theory might work itself out in uncharacteristic ways through the vast times at our disposal. We seem satisfied as long as we can show that fossil organisms and communities worked pretty much as their modern counterparts do. I confess that, as a graduate student, I was so taken by the simplicity and unifying power of "the modern synthesis" that I could imagine no higher task for paleontology than the faithful furthering of its hegemony. The modern synthesis built its theory upon small-scale events that occur within local populations and, assuming a smoothly continuous rather than a hierarchical world, argued for complete extrapolation into millions of years and major transitions in form. Simpson (1944, 1953) supported this position with a "consistency argument" (Gould 1980), not with exclusive demonstration. He showed that nothing in the fossil record precluded a microevolutionary resolution, not that the data required such explanations.

Of course, I have no quarrel with this style of exemplification when we study paleontological events of the static moment—the functional morphology of this trilobite, or the standing crop and trophic interactions of this community at that moment—but I do question its automatic use in our unique domain: the data of *temporal change in geological time*. I believe that our preference for searching always to exemplify microevolutionary principles in the fossil record has been unfortunate for two major reasons:

1. It has led us into serious errors of scaling. We see, in the vastness of geological time, events that bear superficial similarity to phenomena of local populations—and we assign a similar cause without realizing that the extended time itself precludes such an application. Thus, some of the most puzzling phenomena of paleontology, potential sources of new theory, are passively pushed under a familiar rug. To cite three examples:

i) Gradualism. In this case, we didn't even see the phenomenon in fossil sequences, but assumed that it must have existed and been obliterated by an imperfect record—and all because we thought that evolutionary theory (as Darwin falsely claimed) required its generality (Eldredge and Gould 1972; Gould and Eldredge 1977). Thus we ignored as no data one of the most interesting and potentially revealing aspects of the history of most species—stasis. Moreover, we tend to interpret rare cases of gradualism as we would treat an increase of abdominal bristles during 10 generations of conscious selection in a fly bottle—as obvious results of directional selection. And yet, to see gradualism at all in the fossil record implies such an excruciatingly slow rate of per-generation change that we must seriously consider its invisibility to natural selection in the conventional mode—changes that confer momentary adaptive advantages. Any measurable momentary advantage should usually sweep through a population in times represented more nearly by a bedding plane than by a thick sequence. Thus, I believe that sustained gradualism, rare though it may be, represents more of an interesting mystery than a ringing affirmation of microevolutionary extrapolation. Lande (1976), for example, has shown that potentially gradual rates in *Hyopsodus* (Gingerich 1976) are, as a result of their sluggishness, reasonable candidates for genetic drift even in persistently large populations.

ii) Succession. Classical succession theory in ecology refers to orderly changes engendered by organisms themselves and occurring over a time span of perhaps hundreds of years. (Predictability of intrinsic direction in the absence of externally imposed environmental change constitutes the chief fascination of classical succession. Thus, pioneer species arrive first and spread as a consequence of their means of transport, modes of growth and reproductive strategies; but they are predictably replaced either because they "prepare" the substrate for later stages or simply because later stages increase more slowly but prevail in competition.) I don't deny that certain patterns of faunal change, observed over millions of years in geological sequences, offer some interesting analogies to classical succession. But the scale is all wrong; they cannot represent the process itself, and attempts to force such sequences into a successional mold obscure a phenomonon that may be new and revealing.

Bretsky and Bretsky (1975), for example, sampled at up to 25 foot intervals (some shorter) in a late Ordovician succession from the Nicolet River Valley. They found three "successions," each disrupted and reset to lower levels by an "external physical perturbation." They described these sequences in the language of ecological time—speaking (1975, p. 235) of colonization by opportunists, "biological accommodation" between early and late colonizers for high diversity at an intermediate stage, and reduction of carrying capacity at a later stage. Can this be an appropriate terminology for millions of years and generations? Opportunists cannot persist for millennia, if the concept of self-induced change has any meaning. Since the basin of deposition was shallowing throughout their sequence (p. 230), this external effect may have powered the systematic changes that Bretsky and Bretsky observed.

Walker and Alberstadt (1975) distinguish between autogenic (self-induced) and allogenic succession (engendered by changes in the physical environment), and they are sensitive to effects of scale. But they also try to identify true autogenic succession in geological time "in an unchanging environment" (1975, pp. 248–252) over millions of years. Their example, the Devonian Haragan-Bois D'Arc sequence of Oklahoma, spans 100 to 228 feet and cannot represent anything like classical succession, despite Walker and Alberstadt's effort to apply such concepts as pioneer community, opportunism, and biological accommodation. They also present, *en passant,* several observations that belie any rigorous comparison—the "opportunists" of their "pioneer community," for example, are "distributed equally throughout the formation," (p. 252) not concentrated in (much less restricted to) the basal units.

These regular transitions are of great interest and unknown significance, but we will lose their message if we view them merely as exemplifications of wrongly scaled ecological processes, rather than as phenomena in their own right. Rollins et al. (1979) are more sensitive to scaling and the differences between community succession and community replacement. [They also argue (p. 89), wisely in my view, that succession once again be restricted to cases of primarily autogenic control.] They relate their systematic changes to the geological phenomena of transgression-regression and attendant shifting in position of onshore-offshore stress gradients.

iii) Character displacement. This important sign of interaction between species in sympatry can be detected in the fossil record when we find the appropriate analogue to modern settings—the preservation of moments, or strictly limited numbers of generations (Eldredge 1974; Schindel and Gould 1977). But the primary phenomenon that might, superficially, seem to represent character displacement—the gradual separation in morphology of two sympatric species through geological time—simply cannot reflect it at all, for the scales are wrong by orders of magnitude. Gingerich (1976), for example, cited character displacement as the cause of gradual separation between two *Hyopsodus* lineages over millions of years. But the rates of change are so slow that no perceptible differences could have arisen within a generation or two; (character displacement is a rapid event in ecological time, representing the initial interaction of two species upon their first encounter). Gingerich has found a fascinating phenomenon of unknown meaning; it is a challenge, not a comforting affirmation of neontological truths.

2. More seriously, our passive stance before evolutionary theory has made much of paleobiology derivative and dull. As I wrote once before: "Why be a paleontologist if we are condemned only to verify imperfectly what students of living organisms can propose directly?" (Gould and Eldredge 1977, p. 149). Of course, if it is so, then so be it. Not all fields are equal in interest, and we always have a fascinating phenomenology to justify our existence. But I regard it as inherently unlikely that the direct study of vast times has nothing to offer beyond exemplification of a theory developed for events in local populations. (I freely confess that this suspicion arises from my deeper belief, admittedly not a matter of proof or disproof, but rather an organizing vision, that the world is not arranged as a smooth continuum, but as a hierarchy of levels with emergent principles and properties at each level.) I would like to argue that the principle of extrapolation, when proposed by Simpson in 1944, was a progressive and revolutionary view that brought both pride and importance to paleontology—but that it has

now become a stumbling block, and that the seeds for its replacement are available.

Paleontologists before Simpson generally believed that neontological evolutionary theory could not encompass the history of life, and that vast times added a mysterious "something" fundamentally at variance with a Darwinian world view. As to what that "something" might be, they professed ignorance and little hope for resolution. A paleontologist might, using the traditional inductivist methodology, search the fossil record, hoping to enumerate empirical laws dimly reflecting the unknown processes that rendered Darwinsim not merely incomplete, but fundamentally wrong. Beyond this, they could not venture. Thus Osborn, using "facts" of paleontology, firmly rejected the three major evolutionary theories of his day (Darwinism, Lamarckism, and deVriesian mutationism), and offered in return only a few empirical regularities: gradual transition (often across incipient stages of inadaptation), orthogenesis, and a set of new terms for morphological "rules" of transformation. But, as for general theory, he concluded (1922, pp. 141–142):

> We are as remote from adequate explanation of the nature and causes of mechanical evolution of the hard parts of animals as we were when Aristotle first speculated on the subject . . . . I think it is possible that we may never fathom all the causes of mechanical evolution or of the origin of new mechanical characters, but shall have to remain content with observing the modes of mechanical evolution, just as embryologists and geneticists are observing the modes of development, from the fertilized ovum to the mature individual, without in the least understanding either the cause or the nature of the process of development which goes on under their eyes every day.

These claims for an intrinsically separate theory of macroevolution, accompanied by such a pessimistic attitude towards the possibility of ever encompassing it, hardly encouraged hope for an evolutionary synthesis.

Simpson broke with this tradition by arguing that the mysterious "something" was a chimera, and that the fossil record demanded no principles beyond what geneticists had discovered by studying modern populations. This "consistency argument" represented the required counter to an entrenched tradition. Simpson's view had two important consequences: i) It made available to paleontologists a fruitful body of theoretical ideas that their previous traditions had regarded as useless or irrelevant. ii) It provided what may have been the crucial piece toward the construction of one of the most important theories in 20th century science—the "modern synthetic" theory of evolution. For no impediment to a general evolutionary theory could have been more distressing than the claim that our direct record of life's history indicated a fundamental inadequacy for the central claims of that theory.

Yet, as the history of religious and political belief so abundantly shows, fresh and invigorating visions tend to rigidify after they are institutionalized. Later votaries push the line and either forget why it had once seemed so important, or simply lose their excitement. Thus, Simpson's vision of continuity and extrapolation hardened and has come, finally, to restrict paleontological theory rather than to enlarge it.

Textbooks often provide our best insight into standard perceptions. I can't think of any recent event that depressed me more than reading this—the complete, verbatim account of "macroevolution"—in one of the three leading textbooks of introductory biology, and surely the most rigorous among them:

> Each of the examples of microevolution examined, involving shifts in the frequencies of small numbers of genes, could be multiplied a hundredfold from reports in the scientific literature. Biologists have been privileged to witness the beginnings of evolutionary change in many kinds of plants and animals and under a variety of situations, and they have used this opportunity to test the assumptions of population genetics that form the foundations of modern evolutionary theory. The question that should be asked before we proceed to new ideas is whether more extensive evolutionary change, macroevolution, can be explained as an outcome of these microevolutionary shifts. Did birds really

> arise from reptiles by an accumulation of gene substitutions of the kind illustrated by the raspberry eye-color gene?
>
> The answer is that it is entirely plausible, and no one has come up with a better explanation consistent with the known biological facts. One must keep in mind the enormous difference in time scale between the observed cases of microevolution and macroevolution. Under natural conditions the nearly complete substitution of the melanic gene of the peppered moth took 50 years. Evolution of the magnitude of the origin of the birds usually, perhaps invariably, takes many millions of years. As paleontologists explore the fossil record with increasing care, transitions are being documented between increasing numbers of species, genera, and higher taxonomic groups. The reading from these fossil archives suggests that macroevolution is indeed gradual, paced at a rate that leads to the conclusion that it is based upon hundreds or thousands of gene substitutions no different in kind from the ones examined in our case histories (Wilson et al. 1973, pp. 793–794; the second edition merely repeats the paragraphs).

Or this from a recent textbook of evolution (Solbrig and Solbrig, 1979, p. 440):

> The fossil record provides considerable evidence for the soundness of the synthetic theory of evolution. Nevertheless, largely because of the incompleteness of the fossil record and its nonrandomness, fossils do not by themselves provide the proof of evolution, despite widely held belief (sic) that they do. Only the combined and judicious application of data taken from fossils, living organisms, and experiments can provide an approximate justification for Darwin's theory.

Thus, microevolutionary theory is true and sufficient; paleontology's role is to glorify it, however imperfectly.

The philosopher Hegel argued that progressive change tends to occur by a process that he named, with his profession's gift for obfuscation, "negation of the negation." By this, he simply meant that initial *theses* (like Osborn's on the intrinsic separateness of macroevolution) are countered by negations, or *antitheses* (like Simpson's on the complete continuum). Further change usually represents a second negation that does not return to the initial belief, but rather integrates the thesis and antithesis into a *synthesis*. Thus, change is progressive, not cyclical. Although I am no devotee of such metaphysical formulae, I believe that Hegel's insight applies in this case.

I believe that this kind of synthesis is now upon us. Osborn was wrong—or at least he improperly condemned paleontology to intractability—in arguing that an unobtainable theory of macroevolution would be fundamentally contrary to the principles of microevolution. But he was right in claiming that macroevolution had some reasonable claim to theoretical independence. Simpson was right to seek a unified theory on Darwinian principles, but wrong in arguing that the favored style of the modern synthesis—adaptive, gene-by-gene substitution—could encompass nearly everything (as he had come to believe by 1953, though not in 1944—see Gould 1980). A true synthesis would unite Osborn's belief in independence with Simpson's vision of a unified evolutionary theory.

The impediment to such a union has been another "error of logical typing"—in this case, the confusion between principles and their characteristic mode of operation at different levels of the evolutionary hierarchy. I believe that the principles of evolution—mutation, adaptation, natural selection, etc.—are valid and sufficient, thus providing the promise of a unified theory. But they work in different ways, and on different materials, at different levels—and we cannot extrapolate smoothly from one to the next. Thus, adaptation by allelic substitution may explain most change within local populations, but this process cannot be smoothly extrapolated to encompass evolutionary trends, because macroevolution resides on another level of the evolutionary hierarchy (see Eldredge and Cracraft 1980). Changes in populations may arise by allelic substitution; but macroevolutionary changes are a result of the *differential success of species* (Eldredge and Gould 1972; Stanley 1975a). (Moreover, it now appears that speciation itself is not always, or even often, a simple extrapolation of allelic substitution—see my companion piece to this paper. Thus, we must deal with three hierarchical levels—change in populations, speciation, and macroevolution.) Species themselves must enter macroevolutionary theory as irreducible entities (much as alleles do in microevolutionary theory). Their differential origin and survival, and the characteristic amounts of change that accompany their origin (a subject of our profound ignorance at the moment), are the inputs to macroevolution, not the allelic substitutions that adapt local populations to their immediate environment and usually have no macroevolutionary significance at all (since most populations become extinct without speciating).

I seek a kind of "bounded independence" for macroevolution—unity in a body of principles common to all levels, diversity in the different working of these principles upon the material of different levels. In any case, if species are irreducible inputs, then paleontology wins its independence as a subject for the generation and testing of evolutionary theory. The origin of species is the highest, and rarely-observed, event of microevolutionary studies. If we must start with large numbers of species and calculate their differential survival in order to understand macroevolution, then paleontology must be our primary source of information and insight.

This view of macroevolution as differential success of species has major consequences in at least three areas of conventional paleontological study:

(i) Rates or tempos—evolution as a set of infrequent and geologically instantaneous events of speciation, disrupting the stasis of established species that persist with only minor changes during the millions of years that mark their characteristic duration—the theory of punctuated equilibrium.

(ii) Modes—macroevolution as the differential success of species. Trends as a higher order selection upon species functioning as (possibly random) raw material—Wright's rule of random input with respect to the direction of trends (still to be assessed and probably not generally valid), and the theory of species selection. I regard the testing of Wright's rule as a major task for macroevolutionary theory and paleobiology. For the theory of species selection, in its pure form, depends upon it. Consider, for example, a lineage displaying Cope's rule of increasing body size—horses, for example. If Wright's rule be valid, and new species of horses arise equally often at sizes smaller and larger than their ancestors, then the trend is powered by species selection. But if new species arise preferentially at sizes larger than their ancestors, then we don't require species selection at all, since random extinction would still yield the trend. Moreover, the basic Darwinian analogy between mutation in populations and speciation in trends would then fail. In this analogy, speciation plays the role of raw material—random input to a process directed by another force. If mutations were directed preferentially towards adaptation (as in the Lamarckian system), then Darwinism would fail because natural selection could no longer act as a creative force. Likewise, if speciation occurs preferentially in the direction of a trend, no process of species selection is required and macroevolution is not "Darwinian" in this analogical sense.

I can think of many good reasons for suspecting that Wright's rule might not, in general, be valid. In particular, developmental constraints may channel the direction for possible morphological alteration of ancestral species into a set of restricted and narrow routes. The classic literature of heterochrony (Gould 1977) is fundamentally about such channeling. The inherited developmental program of an organism is not a device of unlimited flexibility.

(iii) Explanations of trends. In the conventional model of extrapolated gradualism, trends—since they represent unusually persistent directional selection within a single lineage—must record the increasing "perfection" of organic form, either in adaptation to changing local environments, or in the more cosmic sense of improved general design on engineering principles. This severe restriction in modes of explanation has been a serious impediment to paleontologists; for we can relate few trends to such improvement and have been reduced to pleading ignorance of functional morphology for excusing our lack of success. But if trends represent the differential survival of species, then a panoply of explanations becomes legitimate. Trends may arise simply because some kinds of species speciate more often, or because some kinds live longer than others. And the reasons for more frequent speciation or greater longevity may not reside in morphological superiority, but in characteristic habitats, population sizes, geographic mobility, etc. Morphological shifts may be incidental to the reasons for trends and basically non-adaptive.

Hansen (1978), for example, has shown that early Tertiary volutid gastropods included large numbers of species with either planktonic or non-planktonic larval development. Planktonic species tended to live longer but speciate more rarely since easy dispersal homogenizes populations by gene flow. Non-planktonic species have lower persistence (perhaps as a result of their more limited geographic range), but speciate more frequently, presumably because their local populations are more protected from gene flow by limited larval dispersal. All modern volutes have non-planktonic development. Now is this trend for the replacement of planktonics by non-planktonics to be explained by some intrinsic "superiority" of those that survived? And is this superior adaptation recorded in shifting morphology (average size of protoconch, for example)? I doubt it, although traditional explanations would have proceeded in this way. Indeed, Hansen himself has not broken free from conventional styles in arguing: "It is possible that the planktonics were outcompeted by the nonplanktonics" (pp. 886–887). But I doubt that competition, as usually defined, had anything to do with the trend. The Tertiary included several periods of mass extinction associated with rapid fluctuations in sea level. Non-planktonics might have increased steadily in frequency only because they tended to speciate more often, thereby supplying more inputs to an essentially random process of extinction. (The greater ability of planktonics to persist during "calm" geological times may have been irrelevant to survival during mass extinctions.) Hansen (p. 886) does correlate the major time of gain for non-planktonics with a period "of rapid sea-level fluctuations in the Upper Middle Eocene."

I may summarize this long diatribe by reinvoking the initial question: what shall be our attitude towards biology? We should fish intelligently in its pool of concepts, never fail to ponder how its principles might work differently (or not at all) for events in geological time, recognize that macroevolution has a theory of bounded independence based upon paleontological data, and above all, feed the fishes in return with our own special food.

IV. Goods and Not So Goods

A traditional subject for retrospectives (and prospectives) like this is the assessment of individual subjects for their promise and disappointment. At one extreme, such assessments can be mere personal commentary; at the other, one applies that great criterion of pseudo-objectivity—the questionnaire—and merely reports his colleagues' opinions. I have chosen a rough compromise, perhaps the worst of both worlds. I sent a poor excuse for a questionnaire to 20 invertebrate paleobiologists, using no other criterion than eclecticism and a desire to represent ages, attitudes and concerns as widely as I could. I simply asked them all to list (with or without justification) the 5 subjects of invertebrate paleontology that, in their opinion, had been most fruitful and most diaappointing since the Darwinian centennial of 1959. I shall, in this section, summarize these responses and then, invoking the privilege of all glossators, comment upon them.

My own judgments shall be largely in terms of the two themes motivating this work: (1) the inadequacies of inductivism as a methodology, compared with the strengths of modelling and collection of data in the light of testable hypotheses, and (2) the limitations of extrapolationist biology based purely on microevolution, compared with the promise of paleobiology as the foundation for an independent theory of macroevolution that will strengthen, not compromise, the unity of the evolutionary sciences. I shall also venture some judgments in terms of another chimera too often followed to nowhere—misplaced faith in "reductionist" assumptions that data will be more important as they become more chemical and mathematical (compared with a defense of historicism and holism as not only appropriate but also a source of pride for our subject).

I don't pretend that this "questionnaire" represents any fair sampling of opinion. But one aspect of the exercise did delight me: I received what may be the first 100% response in the history of polling. I take this to mean that our profession is still sufficiently small and personal that anonymity does not intervene to encourage circular filing.

Of 28 subjects mentioned, 12 received a rating in more than ⅓ of the responses. I have divided these twelve into three categories: cheers (no more than 1 negative vote), boos (no more than 1 positive vote) and mixed ratings. As expected, the most interesting subjects fall into the third category.

1. Cheers

i) Paleobiogeography (10 yea, 0 nay). The development of plate tectonics has reoriented our views on the historical biogeography of invertebrate animals.

Although I join in the cheering for this paleobiological spinoff from the greatest event in the earth sciences since the uniformitarian-catastrophist debate, I would not have included it in my first five. The building of a new earth as a framework for the facts of geographic distribution has forced us to rework hundreds of particular examples, but I cannot see that it has been a source of new paleobiological ideas. By appropriate twisting, juggling and special pleading, these facts had formerly been grafted upon stable continents; now we read the same facts in a different and more satisfactory light. The new earth has provided a foundation for important synthesis—but it has been a synthesis of groups and areas, not a production of new and general theory.

I would grant one exception for cases where the new foundation has been presented as a "motor" for general theories of diversity and extinction—particularly Schopf (1974) and Simberloff (1974) on the Permian extinction, and Bakker (1977) for a general model. I do not think it can be coincidental that the greatest extinction of marine invertebrates correlates as well as it does with the coalescence of Pangaea—especially since ecological theory has so much to say about the correlation of organic diversity with area, and since the coalescence engendered such a sharp reduction in the area of shallow seas for a variety of reasons ranging from suturing itself to eustatic draining of the shelves due to collapse of oceanic ridges.

Recently, and with much conscious fanfare (Rosen 1978; Platnick and Nelson 1978), some students of biogeography have been proclaiming a drift-incited revolution in their field via a theory called "vicariance biogeography." The existence of similar creatures on widely scattered parts of the earth constitutes the central problem of biogeography. The initial issue in such cases is taxonomic: are the similarities analogous and due to convergence or homologous and due to common descent. The biogeographic dilemma arises when the similarities are assessed as homologous: how, then, did creatures of common origin get to such different places. Logically, there can be only two solutions—either the animals moved, or the places moved. In a pre-drift geology of stable continents, only the former solution could be considered—hence the classical "dispersalist" biogeography with its panoply of odd modes of transport (hurricanes, floating logs, mud on birds' feet, etc.). In our reconstructed mobile world, the places may move as well, and creatures may find themselves in widely scattered areas not as a result of their own active dispersal, but by passive transport on dispersing areas—the principle of vicariance.

Despite the crusading zeal of its most vociferous votaries, I simply cannot discern any revolutionary import in the notion of vicariance. It is a necessary deduction from the principles and facts of plate tectonics. The real revolution was prior and geological—the theory of plate tectonics itself. I do understand, of course, that the possibility of vicariance forces a reexamination of all classic cases in the biogeography of widely separated, homologously similar organisms, I further understand that the dethroning of dispersal as an exclusive cause also admits vicariance as a hypothesis for smaller-scale events not involving the motion of plates—fragmentation of ranges by such geological barriers as mountain chains within regions, for example. The impact of vicariance will be fruitful and wide ranging. Still, as a theory, it is derivative from a geological revolution.

ii) New techniques of preparation and illustration, including the SEM, treatment of silicified fossils, computer storage and illustration (8 yea, 0 nay—you'd really have to be dyspeptic to vote nay on this item). I can only applaud as well, but I wouldn't have thought to include such as item on my personal list. For me, the excitement of paleobiology during the past 20 years has been engendered by new ideas, not new techniques. Some new techniques force new ideas directly—as when Leeuwenhoek saw his animalcules in a drop of water, and when Galileo realized that the motion of Jupiter's moons would break the crystalline sphere (which, therefore, could not exist). Our new paleontological techniques are important, but they have not had this kind of theoretical impact. (Computers, in permitting the routine handling of large data sets, do represent technology with such impact; but, curiously, only one person mentioned them in this context.)

iii) New publications and convocations—the *Treatise,* the foundation of two paleobiological journals (*Paleobiology* and *Lethaia*), Hallam's volume on *Patterns of Evolution,* two meetings of the NAPC (7 yea, 0 nay). More applause, but not in my list because such vehicles are the products of intellectual excitement, not their causes. Still, the products invigorate the process in return, and we are now in the midst of a welcome loop of positive feedback.

2. Boos

i) Numerical taxonomy (1 yea, 8 nay). I was surprised by the intensity of feeling about an issue I regard as largely passé. I assume that this negative response is not towards the use of statistical information in systematics (an unambiguous plus in my book), but towards the philosophy of numerical taxonomy in its pure and original form (Sokal and Sneath 1963)—the use of copious, unweighted measures of "overall similarity" to construct, with rigorous objectivity, a classification that might be built by an "intelligent ignoramus," trained in the machinery of computation but innocent of expertise about organisms.

I agree with this assessment and regard the failure of numerical taxonomy as an object lesson in what historical scientists should avoid. Its beguiling promise rested on two bad habits of thought: first, the *inductivist* belief that if you can only gather enough pure facts in a rigorously objective way, correct answers can surely be distilled; second, the *reductionist* bowing to conventional prestige relationships among the sciences. By bluff and tradition, mathematics, physics and chemistry hold pride of place. Kelvin terrified Darwin with his short-lived earth constructed from fine physics based on incorrect premises. But Darwin was smart enough to hold firm and to trust natural history. Much fascination with numerical taxonomy rested on a peculiar kind of self-hate—a desire to renounce musty-fusty notions of historical uniqueness, qualitative expertise, and the "feel" of experience, and to substitute for them the rigor of numbers. But history is our business; the subtleties of morphology that teach an expert to assess characters properly for signs of homology are a reflection of that history. Qualitative, historical science is not lesser science; it is different science.

ii) "Reductionist" approaches to fossils, including chemistry, crystallography and the study of shell structure (1 yea, 7 nay). I was surprised and pleased by this strong negative vote: I thought more of our colleagues had been beguiled by the promise of "hard" science. No one doubts the value of all these data, particularly the utility of shell structure in reorienting our ideas on the classification of some molluscan taxa (Taylor et al. 1973); I sense that the disappointment arises because many people expected much more; they assumed that the use of fancy instrumentation and the gathering of data based on microscopic physical and chemical building blocks must yield fundamental insights. Again, this is a delusion born of self-hate and based on the peculiar tendency of poorly-regarded people to assimilate as their own beliefs the ideological instruments of oppression (if anyone can ever explain this bit of bizarre psychology to me, I might begin to understand *Homo sapiens*). Numerical data based on building blocks are different kinds of data, not intrinsically better data. The "underlying" structure of form is not the poorly-preserved chemistry of its parts, but the rules of its formation. Whole animals need to be studied as integrated entities.

iii) Declining emphasis on good, descriptive systematics (0 yea, 7 nay—again, you'd have to be perverse to vote yes, given the construction). In one sense, a justified and serious charge. If new paleobiologists fail to develop and actively exploit an area of empirical expertise in systematics, we will eventually begin to fold in upon ourselves, use and reuse the same inadequate data and finally, like the legendary foo-bird, fly around in ever-tightening circles, until we fly up our own collective asshole and disappear. Yet, in another sense, I regard this common charge as a misplaced response of inductivism to the modelling and hypothesis-testing of modern paleobiology. "More data," and "it's premature" are the standard responses (sometimes justified, but sometimes stifling) of traditional empiricism to a new and valid style of paleontology.

3. Mixed Reviews

i) Studies of the tempo and mode of evolution based upon hypotheses of punctuated equilibrium and species selection (9 yea, 4 nay—undoubtedly unbalanced towards favorability due to identification of the pollster). The recognition of stasis as a real and important evolutionary phenomenon wins highest marks. I argued in the last section that this body of thought might serve as a basis for a new and general theory of macroevolution; this, obviously, is not a dispassionate opinion.

ii) Functional morphology (6 yea, 3 nay). Supporters cite improved understanding of how individual taxa and broader groups functioned; debunkers deplore the speculative quality of some work, based on naive (and downright false) assumptions that everything is adaptive and that natural selection produces optimal design. Supporters and debunkers often have different specific efforts in mind, and yes and no votes do not always refer to the same body of work.

My own increasingly ambiguous feelings about standard functional morphology arise from its failure to generate new theory and its adherence to a conventional attitude that has, in my opinion, been both mined out and overextended. Too much of the work, while elegant in its application and eminently useful in the analysis of individual taxa, has not gone beyond the Newtonian premise that organisms work well. Paley and all the creationists knew this as well as any Darwinian; the theme of good design has not been productive of any new or general insight. Moreover, the premise of good design has often been used as an a priori assumption rather than a hypothesis to be accepted or rejected. In this usage, the premise is unfalsifiable since failure of one adaptive story merely calls forth the invention of an alternative—and scientists have never been short on imagination.

This dilemma can only be averted by a conscious turning away from the rigid adaptationist program that has prevailed within the modern synthesis (Gould and Lewontin 1979). Organisms are not optimizing machines; they are historical objects, constrained by inherited *Baupläne,* modes of development, and mechanical properties of building materials. The answer to why theoretical morphospace is so empty in some places and so chock full in others (surely the cardinal question for a science of form) may have less to do with good performance in the Newtonian sense than with historical and developmental constraints. We need to pay much more attention to the maligned tradition of classical continental European morphology with its emphasis on constraints, history and the formal (rather than functional) properties of design and its generation. (Worse than maligned, it is usually ignored. I doubt that most American paleontologists even know the tradition exists. Very little can be found in English, though see the recent translation by Jefferies of Riedl's important book, 1978.) For this reason, I believe that the most important recent works in functional morphology have been those that, paradoxically perhaps, emphasize the failure of organisms to achieve optimal design as a result of historical constraint (Thomas 1975, 1976, 1978; Stanley 1975b, 1977). Models based on optimal design are most interesting when we can explain why organisms do not match them.

iii) Theoretical and constructional morphology (5 yea, 3 nay). I side stongly with the yeas, and regard this as one of the three most fruitful areas of modern paleobiology. (Stochastic models and macroevolutionary studies of the distribution of tempos and modes win my other votes. All three subjects have been studied by modelling rather than by pure induction, and all have called upon theory at variance with, or tangential too, conventional microevolutionary wisdom.) The methods of theoretical morphology are not games for compelling computers to produce pretty pictures resembling snail shells but attempts to generate complex form with minimal input (see D'Arcy Thompson 1942).

A general theory of form must proceed this way; otherwise, we simply surrender to external complexity. We seek the abstract rules of form in order to learn how their permutation can engender the range of objects that populate our world. Function is another domain—and our nearly exclusive reliance upon it heretofore has precluded an understanding of how form arises (rather than why it is useful). Why's often founder in mists of speculation; how's can be treated rigorously, at least as abstract problems (rules of generation need not correspond to any genetic or developmental mechanism for the construction itself). Anyone who regards this as an abstruse subject with no practical application should study the brilliant work of Seilacher (1970, 1972) and his school—an attempt to combine the European tradition of emphasis on formal properties and constraints with quantitative methods developed in America, and with appropriate attention to function and adaptation as well. Seilacher's analysis (1972) of the construction and utility (including non-utility) of divaricate ornament in mollusks is an excellent place to begin.

iv) Cladistics (4 yea, 3 nay). I have avoided plunging into this Hennigian maelstrom, if only because my own position is so much in the middle. On the one hand, I do not see how the cladistic system can serve as a reasonable basis for classification. It produces wildly unbalanced and unstable higher taxa (any change of opinion about branching sequence early in the history of a group forces a recalibration of all ranks). It also explicitly ignores the biologically important fact that differential amounts of evolution characterize the different forks of a branch (I refuse to abandon the useful notion of "fish" because coelocanths are closer cladistic relatives of humans than of trout). On the other hand, cladistics has yielded important rewards: Branching sequences are potentially objective facts and can, in principle, be reconstructed through the use of shared derived characters. "Overall" similarity, on the other hand, is an invitation to endless wrangling. Cladists have also sharpened our concept of homology, codified the important concept of paraphyly, and correctly emphasized genealogy as the essential notion of *biological* similarity. Finally, cladists have forcefully reminded paleontologists that the criterion of phylogeny is the analysis of characters (Schaeffer, Hecht and Eldredge 1972), not the geological fact of relative occurrence in time. (Think of how many ancestors appear in our imperfect record after their descendants.)

v) Stochastic modelling of diversity (8 yea, 8 nay). No other subject engendered more passion, garnered more votes, or elicited more varied description—from revolutionary theory to arm-waving based on imperfect *Treatise* data. I break the tie, cast my vote with the yeas, but postpone discussion to the next section. Only a few disjointed comments here: (a) Any subject that arouses such interest must be doing something right, even if later judgment rejects its conclusions. (b) These models are attempting to break through a prejudice even deeper than our preference for inductive methods or microevolutionary biology—causal determinism itself and the notion that every ordered pattern must be generated by a definite cause. (c) I reject the most common reason for vociferous opposition—"the data are too imperfect to bear any such analysis"—as a pitfall of inductionism. The data are surely inadequate, but we either work with what we have, trying our best to understand where the imperfections hamper our efforts, or we do nothing. Inductivists often claim that such modelling is a diversion of attention from a primary need to gather data that would permit proper testing of the models. I suspect, however, that debate generated by applying the models to admittedly imperfect information will do more to encourage the gathering of *proper* data than patient, passive and watchful waiting for the process of inexorable accumulation.

vi) Community paleoecology (4 yea, 7 nay). I have already argued that, despite its promise if it would only ask different questions, this subject has floundered on attempts merely to reconstruct the static moment in exquisite detail and upon too uncritical a willingness to apply the concepts of ecological time to events of much longer duration in the fossil record.

V. A Nomothetic Paleontology?

In a classic case of "methinks the lady doth protest too much," historical scientists have given away their disquiet about the validity of their discipline by discoursing at interminable length about the nature, meaning, and methods of their enterprise. Historicity—the necessity of working with complex and unique events in time—constitutes the central dilemma of these sciences. For if science is the search for common pattern in repeated phenomena, what can one do with the fall of Rome or the extinction of *Pharkidonotus percarinatus*? Psychologists long ago coined a pair of opposite terms to express this dilemma, and they have been widely used in other historical sciences, including history itself (Nagel 1952). Among paleontologists, however, they are virtually unknown. Idiographic refers to the description of unique, unrepeated events; nomothetic to the lawlike properties reflected in repeated events. Science is nomothetic insofar as its descriptions include particulars of given times and individual objects only as boundary conditions, not as intrinsic referents in the laws themselves.

I have argued throughout this paper that we should not wallow in self-hate and attempt uncritically to apply to our profession the methods and concerns of "hard" science. I have maintained that we should treasure the legitimate difference between historical and non-historical science, and that we should therefore assert the importance of idiographic description as a scientific activity in its appropriate domain. Nonetheless, I write this closing section to ask whether paleobiology may legitimately be called a nomothetic science as well—and I answer yes. I do not regard this claim as a surrender to "physics envy," but as a statement that properly defines paleontology's position in the continuum stretching from historical to non-historical science. I believe that paleontology should reside right in the middle of the continuum, not at the historical end as most commentators have asserted. Thus, while paleontology must neither ignore nor undervalue its idiographic components, it should search to establish its nomothetic aspects as well. Since our traditional focus has been so idiographic, the nomothetic aspects of paleontology are now in greater need of attention—not because they are more important, but because they have been neglected.

One would have to be a fearful dullard to be unmoved by such stirring bits of idiography as the 50 foot pterosaur, *Archaeopteryx,* and the footprints of *Australopithecus afarensis.* But these events do not intrigue us only for their stunning uniqueness. For me, at least, they are most interesting as embodiments of general, nomothetic principles. The pterosaur tests biomechanical limits of flight and exemplifies principles of scaling and similitude. *Archaeopteryx,* especially if it did not fly (Ostrom 1979), is our premier example of the principle of preadaptation—one of two potential solutions (and the only one favored by Darwin) to the most famous difficulty in applying Darwinism to macroevolution: finding adaptive value for the "incipient stages of useful structures," as Mivart (1871) put it. (Saltational origin of key adaptations is the other solution.) The upright stance of *A. afarensis* was attained so soon after the split of hominids from a common, essentially quadrupedal ancestry with apes (if the biochemical data be valid), that tempos far more rapid than usually envisaged must be allowed even for such extensive anatomical redesigns. In short, all idiographic events have *nomothetic undertones.* These undertones often excite more interest and discussion than the historical character of the event itself.

This citation of nomothetic undertones advances nothing unusual or radical, even though such nomothetics have run a poor and unwarranted second to idiographics for volume of attention throughout the history of paleontology. Recently, however, a far more radical suggestion for a nomothetic paleontology has been advanced. The traditional view admits intrinsic historicity of events and applies nomothetic principles to abstracted aspects. The radical view asks if there might not be a sense—at an appropriate scale of analysis—in which the events themselves are essentially nomothetic in character. That is, might a biological object be treated without reference either to its taxon or to the time in which it lived. Might species be like the molecules of classic gas laws—might they be treated as particles fully comparable one with the other no matter when they actually lived, or what their size, shape, and phylogenetic affiliation? Might a Tertiary clam and an Ordovician nautiloid be reasonably treated as two molecules of hydrogen diffusing from a vessel?

It would, of course, be insane to argue that all uniquenesses adhering to clams, nautiloids, the late Cenozoic and the early Paleozoic be stripped utterly away for all possible subjects of inquiry. This nautiloid in that particular basin probably became extinct for an idiographic reason related both to its biology and its environment. The question, rather, is one of scale. The 19th century scientists who developed much of probability theory were convinced determinists in their ontology. They believed that each throw of a die yielded its result for a definite reason related to a set of factors too subtle and numerous to come under our control, and so varied in their impact that each number, in a long run, came up about the same number of times. Chance models the long run and the large scale accurately, although each individual throw has a determined outcome (even if we don't know how to predict it). Charles Bell, author of the 1833 *Bridgewater Treatise* on the human hand as a manifestation of God's wisdom in its exquisite design, wrote:

> We say, in common parlance, that the dice being shaken together, it is a matter of chance what faces they will turn up; but if we could accurately observe their position in the box before the shaking, the direction of the force applied, its quantity, the number of turns of the box, and the curve in which the motion was made, the manner of stopping the motion and the line in which the dice were thrown out, the faces turned up would be a matter of certain prediction (quoted in Schweber 1977, p. 268).

While Paley—yes, he of *Natural Theology* fame—claimed in 1803: "The cast of a die regularly follows the laws of motion . . . yet because we cannot trace the operations of those laws in the shaking or throwing of the die . . . we call the turning up of the number of the die chance" (quoted in Schweber 1977, p. 268).

A nautiloid species may be like the single cast of a die in its deterministic nature. But we treat it differently because our concerns are not the same. As a vehicle for scientific conclusions (quite apart from its function in a game of craps or monopoly), we do not care about an individual cast. We do, however, care very much about the role of an individual species. It is sufficiently macroscopic, sufficiently peculiar and sufficiently significant to merit our attention—and we therefore focus upon it idiographically, deterministically, and quite appropriately. My complaint is only that we have then tended to extrapolate this idiographic knowability to all possible scales of analysis—although it does not follow that such idiographic determinism must be the most fruitful or interesting approach at other levels.

Just as the determinism of a single cast yields to the stochastic run at a higher level, so too might the total population of species—despite its heterogeneity of taxon and time—be treated with profit as a collection of particles possessing no individual uniquenesses. That is, the real uniquenesses may, in their aggregation as a large sample, match the frequency distributions of random models, just as the distribution of results in tossing coins two, three, four, etc., at a time may be looked up in binomial tables. Thus, using a nomothetics for whole objects themselves, not only for abstracted undertones among their uniquenesses, paleontologists have recently begun applying stochastic models to general problems in the history of diversity (Raup et al. 1973), patterns of extinction (Van Valen 1973), and form (Raup and Gould 1974). Many papers during the first years of *Paleobiology* have discussed, extended, and criticized these themes.

It is hard to imagine a more radical departure from traditional paleontological assumptions based, as they have been, on notions of irreducible uniqueness and the consequent necessity of subdividing the profession by time and taxon, and by training experts accordingly. Thus, this topic achieved the most numerous and evenly divided responses in my survey. Nonetheless, I would like to suggest that random modelling needn't be viewed with such alarm, even by convinced idiographers who intend, with ample justice, to spend their entire lives studying the uniquenesses of taxa and times.

Random models should be viewed as an appropriate tool for paleontologists of all persuasions. First of all, they provide the first explicit set of null hypotheses for assessment of legitimate uniqueness. Since random systems generate a large amount of apparent order, we need to define the bounds of pattern that random systems can produce. More ordered patterns, or lower degrees of order occurring too often must, with respect to the model that generated a null hypothesis, be regarded as nonrandom. Thus, in Bambach's (1977) study of within-habitat diversity through time, low values for the Lower Paleozoic match a nomothetic hypothesis of diversity rising exponentially to a plateau. But higher Tertiary than Mesozoic values do not match a nomothetic world, and we are led to search for a cause specific to Tertiary conditions or taxa. Sepkoski (1979) argues that a single exponential curve cannot match the richness of Lower Paleozoic patterns and he proposes a two-curve model based on the interaction of "Cambrian" and "later" faunas, each with characteristic, idiographic properties. (Here we see an interesting and fruitful interaction of nomothetics and idiographics. The form of the model remains nomothetic—the "real" pattern arises as an interaction between two general curves of the same form, but with different parameters. Idiographic factors determine the parameters and these then enter as boundary conditions into a nomothetic model.)

In many other cases, the world's order remains comfortably within the boundaries of stochastic models and the null hypothesis has not been falsified. I was particularly struck (even awed) to discover that, for all the vicissitudes of times and taxa, the mean center of gravity for Silurian and post-Silurian clades of marine invertebrates (0.4993) so closely matches the predicted 0.5 of the simplest stochastic model—and that the pre-equilibrial clades of Cambro-Ordovician invertebrates and Paleocene mammals, with their fat bottoms in times of rising diversity, fall well below this value (Gould et al. 1977, pp. 37–39). But again, such findings need threaten no one's metascientific faith that God does not play dice. The genus *Nipponites* became extinct for a reason—maybe even for a reason that bears some relation to its bizarre coiling.

And then, of course, the world's frequent fit to stochastic models might mean that ontological randomness really is an admissible way to encompass part of our universe—and that our preferences for determinism are a cultural prejudice born of the idiographics that prevail at the scale of our short personal existence. But this is a metaphysical issue, and science will proceed quite well without the answer that we can never have anyway.

As a final comment, much discussion of this nomothetic approach has, I believe, focussed on the wrong issue—on specific claims, rather than upon fits of data to general models. Thus, the issue of equilibrium, for example, has often been discussed as if such a notion only has utility if diversity has—as a fact—remained nearly constant throughout time. But constancy is a particularistic conclusion that does not flow from the model itself. As its nomothetic content, the model specifies that, after a pool of species reaches carrying capacity, no biological vector calling upon the specifics of taxa and their interactions will produce trends of rising or falling diversity in the presence of unvarying physical conditions. But if physical conditions vary, they will disrupt or reset equilibrium values and species number; if the model be valid, must adjust accordingly. In other words, physical conditions are an *external boundary condition* in the model. Their change resets the system, but does not disturb the nomothetic character of the model itself. If continents drift apart and establish more biotic space by producing more area and engendering higher endemism, then numbers of species should rise without threatening a general notion of equilibrium. If, however, diversity rises as the result of a biotic vector reflecting the idiographic nature of taxa—positive feedback loops between angiosperms and pollinating insects, for example—then the model has failed and the rise is not nomothetic. [Bambach's study (1977) is particularly important because it focuses on within-habitat diversity for unchanging physical space through time.]

Sepkoski (1976), for example, plotted residuals from the species number vs. rock volume regression against inferred area of shallow seas to assess the validity of species-area curves as predictors of diversity. Two periods—the Cambrian and the Triassic—fell well below the line. But these departures from the species-area model affirm rather than compromise the nomothetic claim, because we know that boundary conditions external to the biological model lead to predictions of diversity lower than carrying capacity for these times—the Cambrian as pre-equilibrial, the Triassic as a time of recovery after the Permian debacle. (Quite apart from the specifics of this conclusion, I am delighted to learn that residuals of residuals still preserve such sensible order. It gives me hope that much maligned general data, for all the imperfections of our record, need not misrepresent the history of life.)

When Tom Schopf "commissioned" this article, he sent me a quote from my favorite intellectual, Sir Isaiah Berlin, on the disappointments felt by historians in their failure to construct a nomothetic science of human history:

> All seemed ready, particularly in the 19th century, for the formulation of this new, powerful, and illuminating discipline, which would do away with the chaotic accumulation of facts, conjectures, and rules of thumb that had been treated with such disdain by Descartes and his scientifically-minded successors. The stage was set, but virtually nothing materialized. No general laws were formulated—not even moderately reliable maxims—from which historians could deduce (together with knowledge of the initial conditions) either what would happen next, or what had happened in the past. The great machine which was to rescue them from the tedious labors of adding fact to fact and of attempting to construct a coherent account out of their hand-picked material, seemed like a plan in the head of a cracked inventor . . . . The nomothetic sciences—the system of laws and rules under which the factual material could be ordered so as to yield new knowledge—remained stillborn. (From an essay, "The concept of scientific history," republished in *Concepts and Categories,* p. 110).

Many paleontologists have felt that their science is like history and that its limits are as strict as those so graphically described by Sir Isaiah—if not more so since historians, at least, often work with reasonably complete, eye-witness data, rather than a record characterized preeminently by its imperfections. This is a serious conceptual error encouraged by the historical traditions of paleontology, not by any necessary representation of its status and potential. Paleontology is not a pure historical science; it resides in the middle of a continuum stretching from idiographic to nomothetic disciplines. It possesses a body of idiographic data virtually unparalleled in interest and importance among the sciences—for it is, after all, the history of life. These data must be treasured and touted, but their individuality is not the whole story of our science.

Human history remains so recalcitrantly idiographic because it is the story of a single species—it represents the vicissitudes of an individual (Ghiselin 1974) of unparalleled flexibility. What general theory could encompass it? The history of life has an entirely different nature. It is the story of millions of species all governed by an overarching body of theory—evolution itself. Evolutionary theory must be the center of a nomothetic paleontology, and *paleobiology* must be the locus of its construction. If I had to epitomize the central accomplishment of paleobiology since the Darwinian centennial, I would say that we have overcome the lethargy and despair that motivated the lamentations of Isaiah Berlin and William James for their more idiographic disciplines. The foundations for a nomothetic paleontology have been set—and there is so much more to do.

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Literature Cited

ANONYMOUS. 1969. What will happen to geology? Nature. *221*:903.

AYALA, F. J., J. W VALENTINE, T. E DELACA, AND G. S. ZUMWALT. 1975. Genetic variability of the Antarctic brachiopod *Liothyrella notocordensis* and its bearing on mass extinction hypotheses. J. Paleontol. *49*:1–9

BAKKER, R. T. 1977. Tetrapod mass extinctions—a model of the regulation of speciation rates and immigration by cycles of topographic diversity. Pp. 441–468. In: Hallam, A , ed. Patterns of Evolution. Elsevier; Amsterdam.

BAMBACH, R K. 1977. Species richness in marine benthic habitats through the Phanerozoic. Paleobiology *3*:152–167.

BATESON, G. 1978. Mind and Nature. E. P. Dutton; New York.

Berlin, I. 1978. Concepts and Categories. Viking Press; New York.

Bretsky, P. W. and S. S. Bretsky. 1975. Succession and repetition of Late Ordovician fossil assemblages from the Nicolet River Valley, Quebec. Paleobiology. *1*:225–237.

Bretsky, P. W. and D. M. Lorenz. 1970. Adaptive responses to environmental stability: a unifying concept in paleoecology. Proc. N. Am. Paleontol. Conv. (Part E). Pp. 522–550.

Eldredge, N. 1974. Character displacement in evolutionary time. Am. Zool. *14*:1083–1097.

Eldredge, N. and J. Cracraft. 1980. Phylogenetic Patterns and the Evolutionary Process. Columbia Univ. Press; New York.

Eldredge, N. and S. J. Gould. 1972. Punctuated equilibria: An alternative to phyletic gradualism. Pp. 82–115. In: Schopf, T. J. M., ed. Models in Paleobiology. Freeman, Cooper and Co.; San Francisco, California.

Ghiselin, M. 1974. A radical solution to the species problem. Syst. Zool. *23*:536–544.

Gingerich, P. D. 1976. Paleontology and phylogeny: patterns of evolution at the species level in early Tertiary mammals. Am. J. Sci. *276*:1–28.

Gooch, J. L. and T. J. M. Schopf. 1973. Genetic varability in the deep sea: relation to environmental variability. Evolution. *26*:545–552.

Gould, S. J. 1970a. Evolutionary paleontology and the science of form. Earth-Sci. Rev. *6*:77–119.

Gould, S. J. 1970b. Dollo on Dollo's Law: Irreversibility and the status of evolutionary laws. J. Hist. Biol. *3*:189–212.

Gould, S. J. 1977. Ontogeny and Phylogeny. 501 pp. Belknap Press of Harvard Univ. Press; Cambridge, Mass.

Gould, S. J. 1980. G. G. Simpson, paleontology and the modern synthesis. In: Mayr, E., ed. Conference on the making of the Modern Synthesis. Harvard Univ. Press; Cambridge, Mass.

Gould, S. J., D. M. Raup, J. J. Sepkoski, Jr., T. J. M. Schopf, and D. S. Simberloff. 1977. The shape of evolution: a comparison of real and random clades. Paleobiology. *3*:23–40.

Gould, S. J. and N. Eldredge. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology. *3*:115–151.

Gould, S. J. and R. C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. Proc. R. Soc. London. *205*:581–598.

Hallam, A., ed. 1977. Patterns of Evolution. 591 pp. Elsevier; Amsterdam.

Hansen, T. 1978. Larval dispersal and species longevity in Lower Tertiary gastropods. Science. *199*:885–887.

Kummel, B., ed. 1954. Status of invertebrate paleontology, 1953. Bull. Mus Comp. Zool. *112*:91–317.

Lande, R. 1976. Natural selection and random genetic drift in phenotypic evolution. Evolution. *30*:314–334.

Mivart, St. G. 1871. On the Genesis of Species. 296 pp. MacMillan; London.

Moore, R. C., ed. 1968. Developments, trends, and outlooks in paleontology. J. Paleontol. *42*:1327–1377.

Nagel, E. 1952. The logic of historical analysis. Sci. Monthly, Vol. 74.

Olson, E. C. 1962. Late Permian terrestrial vertebrates: U.S.A. and U.S.S.R. Trans. Am. Phil. Soc. *52*:3–224.

Osborn, H. F. 1922 Orthogenesis as observed from paleontological evidence beginning in the year 1889. Am. Nat. *56*:134–143.

Ostrom, J. H. 1979. Bird flight: How did it begin. Am. Sci. *67*:46–56.

Platnick, N. I. and G. Nelson. 1978. A method of analysis for historical biogeography. Syst. Zool. *27*:1–16.

Raup, D. M. 1966. Geometric analysis of shell coiling: general problems. J. Paleontol *40*:1178–1190.

Raup, D. M. 1975. Taxonomic survivorship curves and Van Valen's Law. Paleobiology. *1*:82–96.

Raup, D. M. 1978. Species diversity in the Phanerozoic: an interpretation. Paleobiology. *2*:289–297.

Raup, D. M., S. J. Gould, T. J. M. Schopf, and D. S. Simberloff. 1973. Stochastic models of phylogeny and the evolution of diversity. J. Geol. *81*:525–542.

Raup, D. M. and S. J. Gould. 1974. Stochastic simulation and evolution of morphology—towards a nomothetic paleontology. Syst. Zool. *23*:305–322.

Riedl, R. 1978. Order in living organisms (translated by R. P. S. Jefferies). 313 pp. John Wiley and Sons; New York.

Rollins, H. B., M. Carothers, and J. Donahue. 1979. Transgression, regression, and fossil community succession. Lethaia. *12*:89–104.

Rosen, D. E. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. *27*:159–188.

Rudwick, M. J. S. 1961. The feeding mechanism of the Permian brachiopod *Prorichthofenia*. Palaeontology. *3*:450–471.

Rudwick, M. J. S. 1964. The inference of function from structure in fossils. Brit. J. Phil. Sci. *15*:27–40.

Schaeffer, B., M. K. Hecht, and N. Eldredge. 1972. Phylogeny and paleontology. Evol. Biol. *6*:31–46.

Schindel, D. E. and S. J. Gould. 1977. Biological interaction between fossil species: displacement in Bermudian land snails. Paleobiology. *3*:259–269.

Schopf, T. J. M. 1972. Models in Paleobiology. 250 pp. Freeman, Cooper and Co.; San Francisco, California.

Schopf, T. J. M. 1974. Permo-Triassic extinctions: relationship to sea-floor spreading. J. Geol. *82*:129–143.

Schweber, S. S. 1977. The origin of the *Origin* revisited. J. Hist. Biol. *10*:229–316.

Seilacher, A. 1970. Arbeitskonzept zur Konstruktions-Morphologie. Lethaia. *3*:393–396.

Seilacher, A. 1972. Divaricate patterns in pelecypod shells. Lethaia. *5*:325–343.

Sepkoski, J. J., Jr. 1975. Stratigraphic biases in the analysis of taxonomic survivorship. Paleobiology. *1*:343–355.

Sepkoski, J. J., Jr. 1976. Species diversity in the Phanerozoic: species-area effects. Paleobiology. *2*:298–303.

Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity I. Analysis of marine orders. Paleobiology. *4*:223–251.

Sepkoski, J. J., Jr. 1979. A kinetic model of Phanerozoic taxonomic diversity. II. Early Phanerozoic families and multiple equilibria. Paleobiology. *5*:222–251.

Signor, P. W. III, 1978. Species richness in the Phanerozoic: an investigation of sampling effects. Paleobiology. *4*:394–406.

Simberloff, D. S. 1974. Permo-Triassic extinctions: effects of area on biotic equilibrium. J. Geol. *82*:267–274.

Simpson, G. G. 1944. Tempo and Mode in Evolution. 237 pp. Columbia Univ. Press; New York.

Simpson, G. G. 1953. The Major Features of Evolution. 434 pp. Columbia Univ. Press; New York.

Sokal, R. R. and P. H. A. Sneath. 1963. Principles of Numerical Taxonomy. 359 pp. W. H. Freeman and Co.; San Francisco, California.

Solbrig, O. T. and D. J. Solbrig. 1979. Introduction to Population Biology and Evolution. 468 pp. Addison-Wesley; Reading, Mass.

Spearman, C. 1904. General intelligence objectivety determined and measured. Am. J. Psychol. *15*:201–293.

Spearman, C. 1937. Psychology Down the Ages. 2 vols. 454 and 355 pp. MacMillan; London.

Stanley, S. M. 1975a. A theory of evolution above the species level. Proc. Nat. Acad. Sci. *72*:646–650.

Stanley, S. M. 1975b. Adaptive themes in the evolution of the Bivalvia (Mollusca). Annu. Rev. Earth Planetary Sci. *3*:361–385.

Stanley, S. M. 1977. Coadaptation in the Trigoniidae, a remarkable family of burrowing bivalves. Palaeontology. *20*:869–899.

TAYLOR, J. D., W. J. KENNEDY, AND A. HALL. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea. Conclusions. Bull. Brit. Mus. (Nat. Hist.) Zool. *22*:253–294.

THOMAS, R. D. K. 1975. Functional morphology, ecology, and evolutionary conservatism in the Glycymeridae (Bivalvia). Palaeontology. *18*:217–254.

THOMAS, R. D. K. 1976. Constraints of ligament growth, form and function on evolution in the Arcoida (Mollusca: Bivalvia). Paleobiology. *2*:64–83.

THOMAS, R. D. K. 1978. Shell form and the ecological range of living and extinct Arcoida. Paleobiology. *4*:181–194.

THURSTONE, L. L. 1924. The Nature of Intelligence. 167 pp. Kegan Paul, Trench, Trubner and Co.; London.

THURSTONE, L. L. 1935. The Vectors of Mind. 266 pp. Univ. Chicago Press; Chicago.

VAN VALEN, L. 1973. A new evolutionary law. Evol. Theory *1*:1–30.

WALKER, K. R. AND L. P. ALBERSTADT. 1975. Ecological succession as an aspect of structure in fossil communities. Paleobiology. *1*:238–257.

WILSON, E. O. ET AL. 1973. Life on Earth. Sinauer Associates; Sunderland, Mass.