Punctuated equilibria: the tempo and mode of evolution reconsidered

Stephen Jay Gould and Niles Eldredge

Abstract.—We believe that punctuational change dominates the history of life: evolution is concentrated in very rapid events of speciation (geologically instantaneous, even if tolerably continuous in ecological time). Most species, during their geological history, either do not change in any appreciable way, or else they fluctuate mildly in morphology, with no apparent direction. Phyletic gradualism is very rare and too slow, in any case, to produce the major events of evolution. Evolutionary trends are not the product of slow, directional transformation within lineages; they represent the differential success of certain species within a clade—speciation may be random with respect to the direction of a trend (Wright's rule).

As an a priori bias, phyletic gradualism has precluded any fair assessment of evolutionary tempos and modes. It could not be refuted by empirical catalogues constructed in its light because it excluded contrary information as the artificial result of an imperfect fossil record. With the model of punctuated equilibria, an unbiased distribution of evolutionary tempos can be established by treating stasis as data and by recording the pattern of change for all species in an assemblage. This distribution of tempos can lead to strong inferences about modes. If, as we predict, the punctuational tempo is prevalent, then speciation—not phyletic evolution—must be the dominant mode of evolution.

We argue that virtually none of the examples brought forward to refute our model can stand as support for phyletic gradualism; many are so weak and ambiguous that they only reflect the persistent bias for gradualism still deeply embedded in paleontological thought. Of the few stronger cases, we concentrate on Gingerich's data for *Hyopsodus* and argue that it provides an excellent example of species selection under our model. We then review the data of several studies that have supported our model since we published it five years ago. The record of human evolution seems to provide a particularly good example: no gradualism has been detected within any hominid taxon, and many are long-ranging; the trend to larger brains arises from differential success of essentially static taxa. The data of molecular genetics support our assumption that large genetic changes often accompany the process of speciation.

Phyletic gradualism was an a priori assertion from the start—it was never "seen" in the rocks; it expressed the cultural and political biases of 19th century liberalism. Huxley advised Darwin to eschew it as an "unnecessary difficulty." We think that it has now become an empirical fallacy. A punctuational view of change may have wide validity at all levels of evolutionary processes. At the very least, it deserves consideration as an alternate way of interpreting the history of life.

Stephen Jay Gould. Museum of Comparative Zoology, Harvard University, Cambridge, Mass. 02138

Niles Eldredge. Department of Fossil Invertebrates. American Museum of Natural History, Central Park West at 79th Street, New York, N.Y. 10024

You have loaded yourself with an unnecessary difficulty in adopting Natura non facit saltum *so unreservedly.*
> *Huxley to Darwin, Nov. 23, 1859, the day before publication of the Origin.*

I see you are inclined to advocate the possibility of considerable 'saltus' on the part of Dame Nature in her variations. I always took the same view, much to Mr. Darwin's disgust.
> *Huxley to Bateson, Feb. 20, 1894*

I. Gradualism and Stasis

In 1944, G. G. Simpson published a book that brought paleontology within the modern synthesis of evolutionary theory. He used his title to identify the principal topics that paleontology might pursue to enlighten evolutionary theory—tempo and mode. But tempo and mode do not share an equivalent status as subjects for study in the fossil record. Tempos can be observed and measured: modes must be inferred, usually from empirical distribu-

tions of tempos. Such inferences, if they are to be made properly, require a random sample of tempos—or at least a sample not hopelessly biased by a priori assumptions about evolutionary rates. Paleontologists have never been able even to approach such a random sample. Our model of punctuated equilibria is a hypothesis about mode. We claim that speciation is orders of magnitude more important than phyletic evolution as a mode of evolutionary change. An unbiased distribution of tempos must be achieved in order to test this hypothesis rigorously.

We may illustrate this dilemma with an analogy from genetics. Population geneticists recognized from the outset that a primary datum of their profession would be a measure of the amount of genetic variability in natural populations. This basic issue could not be resolved simply because no one knew how to take a random sample of genes in order to establish the relative frequency of variable vs. fixed loci. In the absence of direct evidence, two opposing schools (advocates of very limited vs. copious variation) argued for half a century, and their debate set the tone and concern of an entire profession (Lewontin 1974). Impressive catalogues of variable genes had been compiled even before the debate began: geneticists suffered no dearth of evidence for multiple alleles at loci. The problem lay only in the nature of sampling: genetic variation had to exist before a trait could be located—invariant loci could not be identified; hence, no random sample could be drawn. With electrophoretic techniques applied during the last decade (Lewontin and Hubby 1966 et seq. through hundreds of papers), loci can be identified without prior knowledge about their variability. Random samples were established and the central dilemma of population genetics was resolved: variation is copious.

We believe that paleontology has labored under a strikingly similar dilemma. The empirical distribution of evolutionary tempos is as fundamental a datum to our profession as amounts of variability are to geneticists. Yet, just as geneticists could only identify variable traits, paleontologists have worn blinders that permit them to accumulate cases in one category only: they have sought evidence of slow, steady and gradual change as the only true representation of evolution in the fossil record

(Eldredge and Gould 1972). Two other classes of information were explained away or simply ignored: 1) morphological gaps in stratigraphic sequences—which might have suggested a punctuational view of evolution—were attributed to imperfections of the fossil record; 2) evolutionary stasis, though recognized by all and used by stratigraphers in the practical work of our profession, was ignored by evolutionists as "no data." Thus, Trueman rejoiced in *Gryphaea* (1922) but never mentioned the hundreds of Liassic species that show no temporal change. Rowe (1899) monographed *Micraster* but spoke not a word about its legion of static colleagues in the English chalk. In fact, the situation in paleontology is far worse than that confronting genetics a decade ago. At least the geneticists were frustrated by an absent technology: they knew what data they needed. Paleontologists allowed a potent, historical bias to direct their inquiry along a single path, though they could have accumulated other data at any time. What's more, paleontologists accumulated hardly any good examples: the gradualistic idols that were established had feet of clay and rarely survived an intensive restudy. The tale of *Gryphaea* is dead in Trueman's formulation (Hallam 1968; Gould 1972). *Micraster* will soon follow. (Rowe's data identified three successive species, but he had no stratigraphic control for samples within taxa. Even if his gradualistic tale were true—which it is not—his own limited data could not have established it.) The collapse of classic after classic should have brought these gradualistic biases into question. The alienation of practical stratigraphy from an evolutionary science that required gradualism should have suggested trouble (see Eldredge and Gould, in press): always trust the practitioners.

This sorry situation led us to postulate our alternative model of punctuated equilibria (Eldredge 1971; Eldredge and Gould 1972). We wanted to expand the scope of relevant data by arguing that morphological breaks in the stratigraphic record may be real, and that *stasis is data*—that each case of stasis has as much meaning for evolutionary theory as each example of change. We did this by recognizing that the model of speciation preferred by most evolutionary biologists did not yield a prediction of gradual change in large populations. Most evolutionary change, we argued,

is concentrated in rapid (often geologically instantaneous) events of speciation in small, peripherally isolated populations (the theory of allopatric speciation). (Our model of punctuated equilibria works equally well for sympatric speciation when two conditions are met [see Bush et al. in press, for their defense]: daughter species must arise from a small subgroup of the parental population, and they must do so in no more time than it takes for a peripheral isolate to speciate in the allopatric model.) The norm for a species during the heyday of its existence as a large population is morphological stasis, minor non-directional fluctuation in form, or minor directional change bearing no relationship to pathways of alteration in subsequent daughter species. In local stratigraphic sections, we expect no slow and steady transition, but a break with essentially sudden replacement of ancestors by descendants: this break may record the extinction or emigration of a parental species and the immigration of a successful descendant rapidly evolved elsewhere in a small, peripherally isolated population. (Small numbers and rapid evolution virtually preclude the preservation of speciation events in the fossil record; in any case, speciation does not occur in local sections inhabited by abundant ancestors.)

For all the hubbub it engendered, the model of punctuated equilibria is scarcely a revolutionary proposal. As Simpson (1976, p. 5), with his unfailing insight, recognized in three lines (where others have misunderstood in entire papers), our model tries to "clarify and emphasize ideas nascent in previous studies of the synthetic theory." We merely urged our colleagues to consider seriously the implications for the fossil record of a theory of speciation upheld by nearly all of us,* and to recognize the search for phyletic gradualism as a bad historical habit not consistent with modern evolutionary ideas. Nonetheless, we did recognize that our modest proposal suggested two more radical changes in theory and practice:

1) We realized that the extrapolation of punctuated equilibria to macroevolution suggested a new explanation for the fundamental phenomenon of evolutionary trends (Eldredge and Gould 1972, pp. 111–112 and fig. 10, p. 113; Stanley 1975a).

2) We knew that we were proposing a reorientation of empirical work in evolutionary paleontology—away from the search for gradualism in selected species within local sections, towards the quantitative study of evolutionary pattern in all members of a fauna.

An a priori bias toward gradualism as the only "true" evolutionary event continues to preclude any fair test for relative frequency among the possible tempos of evolution. At worst, it dictates an erroneous interpretation of major evolutionary events. Thus, Durham tried to estimate the age of common ancestry for deuterostomes by stacking species end to end in lineages of phyletic gradualism. He specifies 6 m.y. as an average "species duration" and estimates 100–600 durations strung on a line to reach the common ancestor of Early and Middle Cambrian echinoderms. Running further down the string, he places the common ancestor of deuterostomes "slightly over a billion years before the beginning of the Cambrian" (1969, p. 1128)—an age considerably earlier than the most generous estimate now being offered for the origin of the eukaryotic cell (Schopf and Oehler 1976)! Yet Durham states that his estimate can be too great only if he overestimated the number or length of species durations—it never occurs to him that the postulate of gradualism and linear stacking might be fallacious. In fact, he argues that a belief in evolution itself requires his mode of estimate: "Acceptance of the doctrine of evolution and adherence to a biologic species concept and their corollaries necessitates elapse of a considerable interval of time prior to the Cambrian in order for the necessary evolutionary events to have taken place."

At an intermediate level, gradualistic biases inspire misleading tales of continuity in more restricted, empirical studies. Hurst (1975), for example, presents two outstanding figures of gradualism in the *Resserella sabrinae* lineage (Silurian brachiopods from Wales and the Welsh Borderland). These figures (Hurst

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1975, pp. 320–321) display more than 10 samples arranged, so the caption declares, "in chronological order." Hurst depicts only one reversal in an otherwise continuous trend for both characters—impressive examples of gradualism. Or so it would seem, until we read further in the caption and discover that "chronological order" is established by "paleontological and stratigraphic evidence." Some samples are ordered by superposition, and these are indicated on the figures (the one morphological reversal occurs between two superposed samples). We then discover that gradualism itself is the criterion for "paleontological" ordering—hence no reversals, by definition. Moreover, in no fewer than four cases (and for four independent pairs of samples), the "chronological order" of the first figure is exactly opposite to that of the second figure. One may believe in gradualism with all one's soul, but how can temporal order run in different directions for different characters? (We thank G. Klapper for pointing this out to us; we missed it the first time around.)

At best, a gradualistic bias leads to no obvious error but only to the neglect of important evidence for stasis. English-speaking paleontologists have rarely approached the zeal of some continental workers who regard deflections from linear trends as "irregularities in the course of development" ("Unregelmässigkeiten im Entwicklungsablauf," Bettenstaedt 1962, p. 407). But they have bypassed overwhelming evidence for stasis to concentrate on rare cases of gradualism. As Scott (1974, p. 136) admits for Foraminifera: "Because of their stratigraphical value, unidirectional trends in shell morphology have attracted most comment, although it is not established that they are even a principal feature of foraminiferal evolution."

The bias that regards stasis as "no data" persists even within the few satisfactory examples of gradualism known to us. One might have expected that such studies would value all characters equally by attempting to delimit the scope of gradualism among traits within a chosen taxon. Ziegler's celebrated study of the Silurian brachiopod *Eocoelia* (1966), for example, presents data for five graphable characters. Three display a fluctuating pattern, one no trend at all, and the last a directional pattern. Only the last is graphed.

Ozawa (1975) measures nine characters in his exemplary account of the Permian foraminifer *Lepidolina multiseptata.* Four exhibit gradual trends; five do not. The first four are either graphed or listed in tables of mean values; the remaining five are discussed in qualitative terms only.

But stasis will not go away; and the punctuations that mark the fossil record do not smooth out as stratigraphic resolution improves. Even Darwin had to retreat from the lovely tree of pure gradualism that he sketched in the first edition of the *Origin.* For he added to the fourth edition the following proviso: "it is far more probable that each form remains for long periods unaltered, and then again undergoes modification" (quoted in Gingerich, 1976).

II. What Eldredge and Gould Did Not (And Did) Say

Our model of punctuated equilibria has been widely discussed and applied; we also detect a good deal of disagreement about what we actually said. We write this paper as a collective response and amplification. It is not a comprehensive review of the debate between gradualism and punctuation—for this would compel us to chronicle the entire history of evolutionary paleontology. We confine our comments strictly to those who have tried explicitly to test our model and to some earlier papers cited by them, sometimes to support us, but usually to refute us.

Beyond the major substantive criticism that gradualism remains a more adequate model for assessing the history of life (see subsequent sections), the two most frequent criticisms of our paper (Eldredge and Gould 1972) are methodological. In both cases, we feel that we have been misunderstood:

1. Some critics (e.g. Harper 1975) have seen our work as restrictive in scope—as an attempt rigidly to exclude gradualism by establishing a new dogma for evolutionary tempos. Lespérance and Bertrand (1976, p. 610) charge that we have, "in effect, denied the existence of phyletic gradualism in speciation." We have never understood punctuated equilibria in this light. We see it as fundamentally expansive—as a more adequate picture that should extend the range of paleontological activity by valuing types of data

previously neglected. We never claimed either that gradualism could not occur in theory, or did not occur in fact (Eldredge 1971; Eldredge and Gould 1974, p. 307). Nature is far too varied and complex for such absolutes; Captain Corcoran's "hardly ever" is the strongest statement that a natural historian can hope to make. Issues like this are decided by relative frequency. The neoteny of axolotl was proven experimentally in the 1860's, but no one viewed the case as a serious challenge to Haeckel's recapitulation. A few examples of genetic drift do not refute natural selection as the directing force of evolution. The fundamental question is not "whether at all" but "how often." The potential neutrality of many mutations, arising from the redundancy of the genetic code, is another matter. Here we have a challenge based on relative frequency —a claim that *most* genetic substitutions may not be guided by selection.

Our unhappiness with gradualism arose from *its* status as restrictive dogma. For it has the unhappy property of excluding a priori the very data that might refute it. Stasis is ignored as "no data," while breaks are treated as imperfect data. Relative frequency cannot be assessed because contrary data are not presented. All facts are gathered in the light of some theory. The explicit formulation of punctuated equilibria should lead to the casting of a wider net for data to test the relative frequency of evolutionary tempos; for we know no other way to make reasonable inferences about evolutionary modes—specifically, in this case, the relative importance of speciation vs. phyletic evolution. Of course, we do not champion punctuated equilibria as liberal pluralists with no suspicion about the final outcome. We do regard punctuated equilibrium as by far the most common tempo of evolution—and we do assert that gradualism is both rare and unable in any case—given its characteristic rate—to serve as the source for major evolutionary events (pp. 133–134).

We are gratified that many paleontologists have used our model to expand a range of concepts and data. Sprinkle (1976), for example, realizes that it comfortably permits the designation of small, but very distinct Paleozoic echinoderm clades as classes. Walker (1975) and Pilbeam (1975) have supported the utility of stasis in tracing phylogeny:

Using the gradualistic model to the full, it would be possible, given the enormity of geological time, to derive practically any modern species from practically any fossil one. Using the punctuated equilibrium model we should be able to observe the stasis in each recorded species and develop our phylogenetic schemes accordingly (Walker 1975, p. 7).

2. In a misinterpretation inspired largely by our own ambiguity, many critics have attributed to us a notion of testability that we wish decisively to reject. Some have claimed that we abjure testability altogether in asserting the necessary truth of punctuated equilibria. Scott (1976), for example, charges that we dismiss gradualism "without trial of the stratigraphic evidence." We made no such claim; we merely supported the general statement about science—defended by all its astute historians and philosophers (Kuhn 1962; Hanson 1969, for example)—that observation cannot be "objective," but must be made under the aegis of some theory. This is no denial of testability; it only asserts that data to refute a theory must usually be gathered in the light of an alternate theory. We proposed punctuated equilibria in order to permit the test, not to avoid it! The empirics of the case should prove our adherence to the cardinal principle of testability. If we thought that no stratigraphic evidence were needed, we would not have presented quite a bit of it ourselves (Eldredge and Gould 1972, pp. 98–108). If most paleontologists viewed our model as untestable, we would not be writing this paper —for there would be no extensive literature on explicit, putative tests to inspire this commentary (e.g. Johnson 1975, p. 648 on the deduction of three predictions from our model and their test in the stratigraphic record).

Others have recognized our adherence to the principle of testability, but have interpreted us as stating that fossil evidence can decide nothing of importance in evolutionary theory—that all decisions must be made by evolutionary theorists working with living organisms (Roughgarden 1973, p. 225; Kitts 1974, p. 471; Stanley 1975, p. 646). The offending statement in our paper follows; if time could move backward and if Omar Khayyam had not written so truly about the moving finger, we would value the opportunity to re-

write it: "We can apply and test, but we cannot generate new mechanisms. If discrepancies are found between paleontological data and the expected patterns, we may be able to identify those aspects of a general theory that need improvement. But we cannot formulate these improvements ourselves" (1972, pp. 93–94). Our critics have taken this as a general statement about paleontology. Sylvester-Bradley (in press, p. 42), though he likes our model, charges us with "a defeatist attitude, which suggests that paleontology can never decide which theory is wrong." Roughgarden writes (1973, p. 225): "On its face the commitment is false, for it is possible that paleontologists could be the first to discover causal mechanisms with long time constants." Kitts replies (1974, p. 471): "Why can't paleontologists formulate theoretical improvements themselves? . . . Paleontological events may legitimately be used to test the long range historical consequences of evolutionary theories."

We agree with Kitts and Roughgarden. We, with our primary interests in evolutionary theory, would never have become paleontologists had we regarded the data of our field as fundamentally unavailable for evolutionary insight. Of course the data of paleontology will inspire macroevolutionary theory and play a major role in testing it. Where else would we go?

Our statement, as cited above out of context, seems to be a general indictment of paleontological potential. In the context of its paragraph, however, we can only read it as we intended it—as a limited statement treating one issue only: microevolutionary theories about the mechanisms of speciation. We will stick by this limited intent: fossils alone will neither decide the issue of how speciation occurs, nor will they, *by themselves*, supply the information needed to infer new mechanisms.

We could not be more optimistic about paleontology and its potential, yet unrealized, role in evolutionary theory. In exhorting paleontologists to leave microevolutionary theory largely to neontologists, we merely tried to assert the inviolability of our own, extensive turf—time.

III. Testing Punctuated Equilibria

A) *Introduction.*—The model of punctuated equilibria is eminently testable. It would be

a sad commentary indeed on the status of paleontology if so basic an item as the probability distribution of evolutionary tempos could not be reasonably inferred from the fossil record, and once we learn something about the distribution of tempos, we will be able to make strong inferences about modes. As Sylvester-Bradley writes (in press, p. 63): "If the punctuation is real, so is the grammar and syntax."

Two general strategies are available: 1) Build towards a distribution inductively by examining individual cases with optimal features: For satisfactory tests, we must work with species-level lineages well preserved over the full span of an extensive geographic and temporal range (see Eldredge 1974, p. 479). (Imperfect cases also provide useful data: we would love to know whether most species sporadically preserved in local sections display stasis [as we suspect], significant fluctuating change, or directional evolution.) Most commentary on our model has involved its application to individual cases; we will record our opinion of these works in the following subsections. 2) Devise more general tests based on quantifiable features of entire clades or communities: In supporting our model, Stanley (1975) has recently proposed four such tests. His last "test of generation time" rejects the gradualistic inference that a correlation should exist between length of generations and macroevolutionary rate. If frequency of speciation controls the rate of evolution, then no such correlation should be expected. We do not regard this test as conclusive because gradualists can claim that a number of effects—variation in the intensity of natural selection in particular—overwhelm the real correlation between generation and rate, and swamp it out completely in actual data.

Stanley's first three tests (adaptive radiation, Pontian cockles and living fossils) address the same issue: major morphological evolution must occur by repeated, rapid speciation since too little time is available for change by standard, gradualistic rates. (Living fossils represent the flip side of arguments from adaptive radiation—morphological change is slow because lingulae and their allies have never been diverse.) We were first inclined to judge these tests as inconclusively directed against a straw man of extreme grad-

ualism—surely, most gradualists would not try to build an adaptive radiation without an unusually high rate of speciation; they would insist only upon the V-shaped pattern of continual divergence between parental and daughter species. We are no longer so certain that Stanley's gradualist is an extremist. Durham (1971), as cited on p. 117, depicted a monumental adaptive radiation by end-to-end stacking of species, without any increase in rate of speciation or phyletic evolution. And Gingerich (in press) has denied any increase in rate of speciation for the great Paleocene-Eocene mammalian transition that yielded rodents, primates of modern aspect, bats, primitive Carnivora, artiodactyls and perissodactyls. He postulates a late Paleocene climatic deterioration, driving the ancestors of these groups into limited Central American spaces where reduced populations subject to severe competition evolved under such intense selection that phyletic change alone yielded the required transitions.

B) *Invalid claims of gradualism made at the wrong scale.*—The model of punctuated equilibria does not maintain that nothing occurs gradually at any level of evolution. It is a theory about speciation and its deployment in the fossil record. It claims that an important pattern, continuous at higher levels—the "classic" macroevolutionary trend—is a consequence of punctuation in the evolution of species. It does not deny that allopatric speciation occurs gradually in ecological time (though it might not—see Carson, 1975), but only asserts that this scale is a geological microsecond. Our model must be tested at the appropriate scale—by considering tempos of change in species and in the process of speciation during geological time.

1. Scales too microscopic: Against our model, Hecht (1974) offers all the evidence of Darwinian, neontological gradualism: "Phyletic transformation can be seen in the *Drosophila* population cage and in the development of domestic types of animals and plants" (Hecht 1974, p. 300). Of course—and at rates that would propel a peripheral isolate to full speciation in a geological instant.

Hecht then sics the polar bear upon us. *Ursus maritimus* evolved from an isolated subpopulation of Asiatic brown bears that invaded tundra and ice-pack areas in Cromer-Mindel times. Against the punctuational view,

Hecht writes (1974, p. 302): "The morphological trends within *U. maritimus* affected the entire population. . . . The changes within the polar bear are classical phyletic transformational changes." But we could scarcely ask for a better case of rapid, allopatric speciation. The "entire population" *is* a small, peripheral isolate (Hecht estimates the breeding population of females at never more than 6,000), and it speciates rapidly.

Hayami and Ozawa (1975) present a similar case, not as a counterexample, but as complementary to our larger aim of legitimizing punctuational events in Darwinian terms. They trace the introduction and gradual increase, beginning in the middle Pleistocene, of a discrete phenotype within populations of the scallop *Cryptopecten vesiculosus*. The pattern of increase in frequency is gradual, but it does not confute our model for several reasons:

i) The change was rapid compared to the duration of most species; in Recent populations, the new phenotype seems to have stabilized at a frequency near 40 percent.

ii) The change has nothing to do with speciation: it is a minor event (an allelic substitution in Hayami and Ozawa's view), occurring in thousands of years, within a lineage destined—like all lineages—for extinction unless it produces daughter species.

iii) The geological pattern of change is not morphological intermediacy, but the sudden introduction and subsequent increase of a discrete phenotype. Traditional paleontologists would recognize two species with overlapping range zones. Thus, as Hayami and Ozawa (1975) argue (see also Hayami 1973), allelic substitution can act as a Darwinian mechanism to produce geological patterns of punctuation.

2. Scales too macroscopic: Sequential species in a larger clade often display continual transition for some traits of their mean morphologies. How could it be otherwise? In a sequence of three, taking the initial point as given, unidirectional trends occur with a probability of 1 in 4 for any character. (One in 2 might be a better figure since we test for unidirectionality by asking whether the third species continues a tendency set by the first two as given). For a sequence of four species, the chance of unidirectionality is 1 in 8, or 1 in 4 by the second argument. Since most sequences are short, and since organisms have an abundance of characters, we expect numerous uni-

directional "trends" on purely stochastic grounds.

These cases are irrelevant to the issue of punctuated equilibria. Yet the majority of claims for gradualism are based on such discontinuous, unidirectional series of discrete steps. These sequences test nothing, for the crucial data lie unreported in the blank spaces between successive species (Eldredge 1971). Our model predicts that these trends reflect the differential success of phenotypic subsets within an essentially random pool of rapid speciations (see Eldredge and Gould 1972, pp. 111–113; Stanley 1975; and part IV of this work). Gradualism, on the other hand, requires insensibly even transition both within and *between* taxa in the sequence. The remarkable fact that such blatantly inadequate data have been so widely accepted as convincing proof of gradualism only reinforces our claim that gradualism has always rested on prior prejudice rather than paleontological data.

The *Micraster* sequence of the English Chalk has resisted the fate of other famous gradualistic tales. Rowe's story (1899) remains unchallenged as the exemplar of gradualism in the English literature. Yet an examination of Rowe's data reveals that it tests nothing of the sort. Rowe had no stratigraphic resolution within these species of heart urchins; his celebrated story is a sequence of three discrete points—named, with a good deal of taxonomic panache, the bull's heart, the turtle's heart and the eel's heart (*M. corbovis*, *M. cortestudinarium*, and *M. coranguinum*). Some traits are unidirectional through the series of three, and almost all of these reflect the same basic feature: increasing complexity of pustulation and surface ornament. Others, equally important, show no trend at all (the middle species, *M. cortestudinarium*, is elongate and rectangular, while both its "ancestor" and "descendant" are shorter and heart-shaped).

Many cases, cited explicitly against our model, are equally irrelevant to its test. Scott (1976), for example, presents Drooger (1963) on the evolution of myogypsinid forams as a primary example of gradualism. But Drooger's work treats evolutionary trends in a large clade of 29 species and cites no evidence for bed-by-bed gradualism within taxa. Drooger presents only one plot in stratigraphic

order (p. 336, the others are drawn as bivariate "growth" diagrams); even the most ardent gradualist will find this figure, to say the least, inconclusive. Finally, as a lovely illustration of a priori bias, we cite Drooger's way of telling us that he has not detected gradualism (1963, p. 319): "It might be possible that the trend towards reduction of the total number of spiral chambers in this oldest group was less rigorous."

Johnson, though a strong supporter of our model (1975), cites among rare counter-cases two of his own works (Johnson et al. 1969; Johnson and Norris 1972). But both involve only a shift in mean morphology among three sequential species of Devonian brachiopods; neither includes any evidence for bed-by-bed gradualism within a species. *Tecnocyrtina missouriensis*, for example, split from *Cyrtina* in the late Middle Devonian, presumably by allopatric speciation (Johnson and Norris 1972). In so doing, it developed plications on its fold and sulcus. The claim for gradualism rests only upon the observation that a subsequent, non-overlapping species, *Tecnocyrtina billingsi*, evolved even more plications. Given a gradualistic assumption that morphologies will alter from bed to bed, we remind readers that it had a 50-50 chance of so doing in the simplest, coin-flip model of random processes.

C) *Invalid claims of gradualism based on inadequate data.*—We have been struck by the extreme ambiguity (to our admittedly biased eyes) of several cases advanced as contrary to our model. The data are consistent with a variety of evolutionary schemes, and exclusively gradualistic interpretations can only arise from fervent desire. Makurath and Anderson (1973, see also Eldredge 1974 and Makurath 1974), for example, search valiantly for gradualism in three successive samples of the Devonian brachiopod *Gypidula*. Their oldest sample, *G. prognostica* from the Keyser Formation, is an agglomeration of 52 specimens from Hyndman, Pa. and 11 from Warm Springs, Va. The middle sample contains 79 specimens of *G. coeymanensis* from the Lower Coeymans Formation near New Salem, New York. Ninety specimens, also of *G. coeymanensis*, define the upper sample (Upper Coeymans Formation, Cherry Valley, New York). Eighty feet of section separate middle and upper samples; at least as much (by in-

ference) separate lower and middle. This is scarcely a bed-by-bed compilation.

Makurath and Anderson make only two closely-allied measurements: spondylium width (y) and beak length (x) as "an estimator of spondylium length" (1973, p. 305). They begin by computing allometric regressions, obtaining slopes of .98 for the lower sample, 1.31 for the middle, and 1.35 for the upper. No gradualism; the samples seem to separate into their two designated species. Then they compute a distance matrix, and calculate 48.89 between lower and middle, 35.46 between lower and upper, and 11.48 between middle and upper. Again, no gradualism; in fact, the lower sample is closer to the upper than to the middle!

Still searching for gradualism, they perform a canonical analysis on their two variables (Fig. 1). Once again, they find no gradualism in projections on either axis or in the general distances. Only the mean shape ratio (Fig. 1) changes in a unidirectional manner. (One scarcely needs the multivariate apparatus of canonical analysis to find this out; the simple calculation of y/x would suffice.) They interpret these differences in shape as "real," even though they are no larger than the differences in size between middle and upper samples "interpreted as functions of sampling" (1973, p. 308), presumably because they confute the gradualistic interpretation. Makurath and Anderson conclude (1973, p. 309): "The shape change trend persists between species and between successive populations of the later species. Speciation in gypidulid brachiopods thus provides an example of phyletic gradualism."

But what are we to make of such limited and ambiguous information? The authors present only three samples with no control of geographic variation (beyond a dubious agglomeration of distant collections into a single sample). Given the limited set of alternatives, it is not particularly impressive that a third sample continues a "trend" set by the first two. The "trend" reflects only one ratio measure of shape; parameters of ontogenetic growth display no gradualism, and general distances refute it. If the major force of Makurath and Anderson's argument lies in their claim that an intraspecific trend (middle to upper sample) follows the same direction set by the species' origin, then we reply that
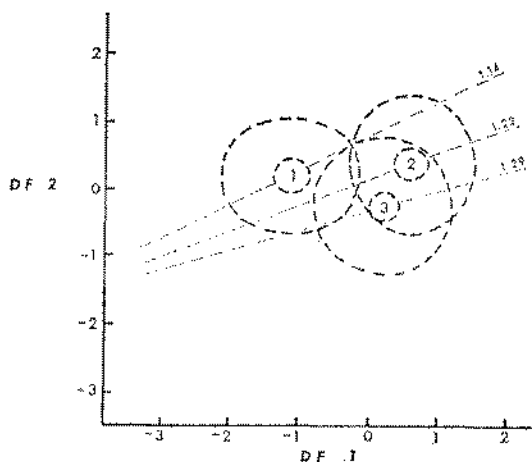

FIGURE 1. Three samples of *Gypidula* plotted on two canonical axes for two original variables. From Makurath and Anderson 1973. Numbers are centroids of the three samples in stratigraphic order; inner circles are 95% confidence intervals; outer circles represent one standard deviation around the mean canonical values. Dotted lines are contoured values of the simple shape ratio, y/x, plotted with respect to the axes. Although we see gradual change in the mean shape ratio, we find no gradualism for projections of centroids on either axis, or for general distances between centroids.

differences in shape between middle and upper samples may represent two points in the normal spectrum of geographic variation existing at all times in *G. coeymanensis*, and utterly unexamined in this study.

Klapper and Johnson (1975) present their study of the Lower Devonian conodont *Polygnathus* partly as a test of our model and an affirmation of phyletic gradualism. They rely, in small measure, on traditional arguments for intermediacy in supposed phyletic transitions, but more importantly on their own criterion for speciation by gradual separation of sympatric populations. This criterion involves the search for "y-branched" phyletic patterns (1975, p. 66), defined as "lineage splitting characterized by an interval of stratigraphic overlap of the ancestral and descendant species, and by accompanying intermediate forms" (p. 66). We are dubious enough about this criterion, since the presence of two species accompanied by intermediates is, among living organisms, more often a sign of hybridization than of incipient divergence. Moreover, Klapper and Johnson claim to find the same y-branched event occurring in many far
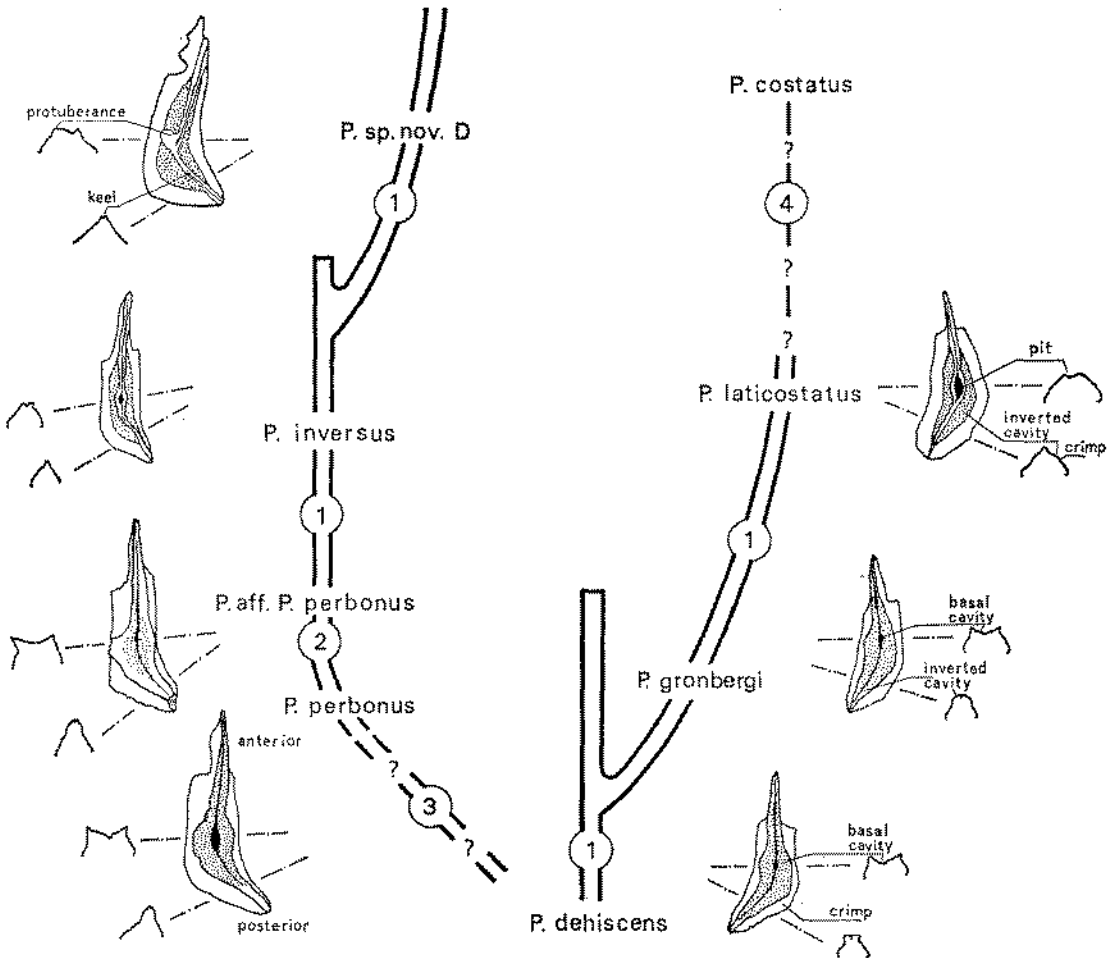
FIGURE 2. The phylogeny of *Polygnathus* as presented by Klapper and Johnson 1975. Numbers 1–4 indicate Klapper and Johnson's assessment of the quality of evidence for their conclusions. We confine our comments to all events in their categories 1 and 2—i.e., all events depicted by them with solid lines (not dashes or question marks).

flung areas. We know no model of sympatric speciation that postulates such in situ divergence on a global scale. But we let these theoretical objections pass, and analyze only the fit of Klapper and Johnson's own evidence to their phyletic conclusions.

Klapper and Johnson epitomize their conclusions in an evolutionary tree, unambiguously presented (Fig. 2). These are diagrams that work their way into textbooks, there to convince the uninitiated that paleontologists can specify with assurance the (gradualistic) history of life. But let us examine all of Klapper and Johnson's evidence for all four evolutionary events depicted without question in Fig. 2: (Klapper has written [personal

communication] that he regards only the "y-branched" patterns, i and iv, as exceptions to our model).

i) the y-branched pattern, as *P. gronbergi* departs gradually from its ancestor *P. dehiscens*.

ii) the gradual phyletic transition from *P. gronbergi* to *P. laticostatus*.

iii) the phyletic transition from *P. perbonus* to *P. inversus* through an intermediate form, *P. aff. P. perbonus*.

iv) the y-branched pattern, as *P. sp. nov. D* diverges gradually from *P. inversus*.

i) Klapper and Johnson cite only three sections to support y-branched gradualism (p. 68). In the first, ancestral *P. dehiscens* is fol-

lowed by intermediates. In the second, beds that should contain intermediates bear no *Polygnathus* at all. In the third, both species are found together, apparently without intermediates. No other evidence is cited. From such scrappy data it is hard to see how anyone could derive with confidence the gradualistic interpretation of Fig. 2—unless one were predisposed to gradualism from the start. Klapper and Johnson conclude (1975, p. 68): "This stratigraphic overlap suggests a 'Y-branched' evolutionary pattern. *P. gronbergi* represents a relatively minor, but discernible morphologic modification from *P. dehiscens*, chiefly involving the beginning of inversion at the posterior end of the platform." We do not wish to invade the taxonomic prerogatives of specialists in groups foreign to us, but we cannot help wondering whether *P. gronbergi* is really a good taxon at all.

ii) We quote verbatim the only cited evidence for gradual transition between *P. gronbergi* and *P. laticostatus* (p. 68): "*P. laticostatus* succeeds *P. gronbergi* at Lone Mountain. A *specimen* [our emphasis] occurs in LM 18, which has a lower platform surface like that of *P. laticostatus* and an upper surface like that of *P. gronbergi*, therefore suggesting a transition between the two species." No further comment.

iii) Some of Klapper and Johnson's arguments are circular—from gradualistic presuppositions to gradualistic conclusions (based on the presuppositions, not on fossil evidence). *P. perbonus* is only known from Australia. Yet, Klapper and Johnson choose it rather than the local Nevadan *P. gronbergi* as an ancestor for *P. inversus* for the following reasons (p. 68): "We do not favor an alternate origin of *P. aff. P. perbonus* (and consequently *P. inversus* from *P. gronbergi*, because at Lone Mountain there is no evidence of transitional forms between *P. gronbergi* and *P. aff. P. perbonus*. Thus, *P. aff. P. perbonus* appears abruptly at Lone Mountain." But our model of punctuated equilibria predicts that no transitional forms will be found between ancestors and descendants in local sections. Our model cannot be falsified by citing the very evidence it predicts, and then choosing gradualistic explanation based on hypothetical ancestors half a world away.

iv) Klapper and Johnson champion this case of Y-branched gradualism because its evidence supposedly arises from three areas so widely dispersed that local origin by allopatric speciation becomes impossible: Nevada, Yukon Territory, and Australia. But the Australian section only yields an overlap in range with no intermediates. The Yukon section contains both species in sympatry with intermediates (no biometrical confirmations are presented). These intermediates could be hybrids or unusual variants of one or the other taxon. A third Nevadan section again contains both species in sympatry with no intermediates. In the fourth Nevadan section a large sample of ancestral *P. inversus* includes some individuals tending towards *P. sp. nov. D*; Klapper and Johnson present no evidence to test the likely possibility that these variants lie within the normal range of *P. inversus*. Higher in the section, *P. sp. nov. D* occurs alone. Again, we do not understand how anything other than prior preference could dictate the exclusive choice of gradualism as an interpretation for such limited and ambiguous data.

In summary, we cited the evidence of *Gypidula* and *Polygnathus* in detail not primarily to reveal the fragility of stories built upon it; for most "phylogenies" based on fossils rely on flimsy data. Rather, we wish to demonstrate that most cases presented as falsifications of punctuated equilibria are circular because they rely, for their gradualistic interpretations, not upon clear evidence, but upon the gradualistic presuppositions they claim to test.

D) *Potentially valid (but mostly unproved) cases of gradualism.*—Among the few potentially valid cases urged against our model, we find only one (Ozawa's forams) that meets all criteria for an adequate test—good geographic coverage, long sequence of closely spaced samples, unambiguous definition of taxa, and adequate biometrical testing on sufficiently large samples. Two others (Kellogg's radiolarians and Gingerich's mammals) are of particular interest because they include a long suite of samples treated biometrically.

A few additional cases fit a gradualistic interpretation better than any other, but do not contain enough data to convince. Ziegler's (1966) celebrated study of the brachiopod *Eocoelia* from Upper Llandoverian strata of the Welsh borderland documents a "progressive suppression of ribs" (1966, p. 523) among
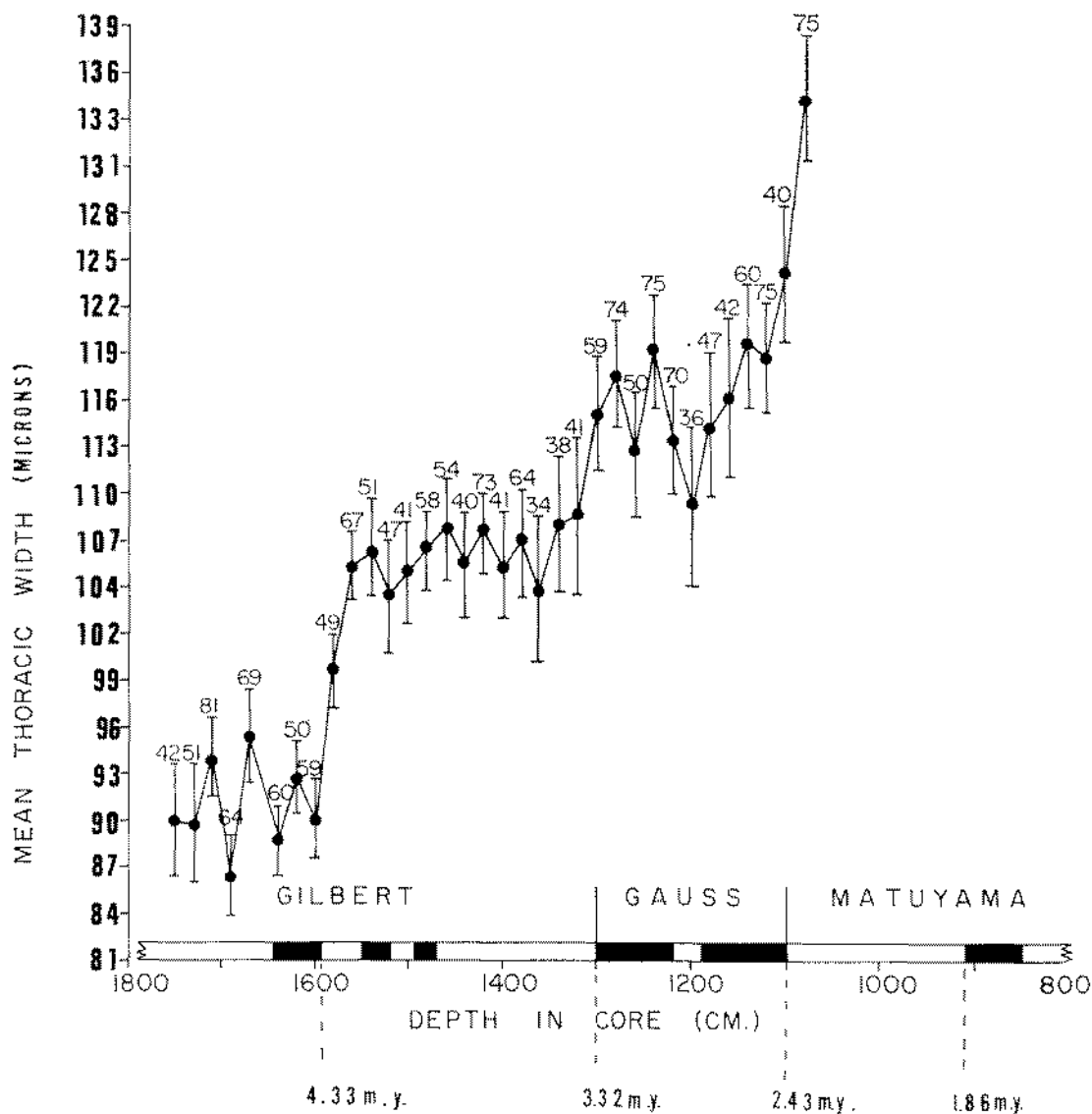
FIGURE 3. The phyletic pattern of change in the radiolarian *Pseudocubus vema* from core E14-8; from Kellogg 1975. Vertical lines through points are 95% confidence intervals for means; numbers above lines represent the sample size.

four successive species in 14 samples. Of four traits treated quantitatively, only the height/width ratio of ribs exhibits a consistent trend among all species (modal rib number increases then decreases, size does the same, while the angle enclosed by six ribs first decreases and then increases). For the height/width ratio, 6 of 14 samples have 6 or fewer specimens, while only three have more than 15 (20, 25, and 39). Coefficients of variation range up to 51 within samples.

Hurst (1975) studied the delthyrial-width/length-of-delthyrial-chamber ratio in 11 samples of the *Resserella* lineage from Wenlockian and Ludlovian strata of Wales and the Welsh borderland. The first four samples show no trend. Only one sample contains more than 10 specimens (18), while 8 of 11 include 6 or fewer, and six (i.e., more than half the samples) contain four specimens or fewer.

1. Kellogg's radiolarians. Kellogg (1975, p. 359) bases her claim for "a long-term phyletic

TABLE 1. Seven selected samples chosen non-randomly to illustrate the evolution of thoracic width in *Pseudocubus vema.*

Chosen by Kellogg			Chosen by us		
Depth in core (cm)	interval between samples (cm)	mean width (microns)	Depth in core (cm)	interval between samples (cm)	mean width (microns)
1750	150	89.81	1710	110	93.79
1600	40	89.92	1600	60	89.92
1560	220	105.67	1540	100	106.84
1340	60	108.28	1440	80	105.71
1280	135	117.41	1360	120	104.23
1145	60	119.33	1240	117	119.16
1085		134.67	1123		118.58

trend in a continuous fossil sequence" on 2 m.y. of the radiolarian *Pseudocubus vema* from a single antarctic deep sea core (Fig. 3). We applaud this excellent study, with its careful collection and presentation of copious data from what are probably the most continuous sedimentary sequences in the geological record. Though we cheerfully admit our prejudices, we find it hard to view Kellogg's pattern (Fig. 3) as anything but a series of three plateaux, periods of stasis interrupted by very rapid rates of change, all admittedly in the same direction. (We argued on pp. 121–122 that unidirectionality of mean points in short sequences is no test of gradualism). Indeed, Kellogg admits that her trend is " 'stepped' rather than straight" (1975, p. 367). Nonetheless, she writes (1975, p. 366): "The single feature which dominates both is a strong trend toward increased size running the entire length of the stratigraphic range of *P. vema* within the core." In her tabular calculation of evolutionary rates (1975, p. 365), Kellogg selects 7 of her 34 samples to display a continuous increase in thoracic width (Table 1). If we select a different seven, spaced even more regularly through the core, we note four decreases with only two increases (Table 1). Our samples are, of course, selected a priori to fit our biases—decreases within plateaux and increases only between them. But hers are equally selected to suit her interpretation —and this is the only point we try to make in Table 1.

From data kindly supplied by Dr. Kellogg, we have computed least squares regressions of mean width vs. depth in the core for each of the three apparent plateaux. We omit 3 of 34 samples as representing intermediate periods of rapid transition—the last two, and

the single sample (9th from the left on Fig. 3) between plateaux 1 and 2. We work against our own hope of zero slopes by recognizing no intermediate samples between plateaux 2 and 3. Samples 1–8 from the first plateau, 10–22 the second, and 23–32 the third. We compute the following three relationships, all with positive slope, but none anywhere near a statistically significant difference from zero;

$$Y = 31.19 + .00129X \text{ for the first plateau}$$
$$Y = 36.35 + .00286X \text{ for the second}$$
$$\text{and}$$
$$Y = 39.46 + .00434X \text{ for the third}$$

(width in micrometer units at 2.9 to the micron, depth in cm). A hypothesis that *all* increase in width occurred only during very brief periods of rapid change between plateaux is fully consistent with the data. Since the punctuations occur within a plexus of predominantly asexual clones rather than between reproductively isolated taxa, we cannot fit them strictly within our model (but see pp. 141–142). We restricted punctuated equilibria to conventional speciation in sexually reproducing Metazoa (Eldridge and Gould 1972, p. 94), but we believe that the general phyletic geometry of long stasis (or mild, directionless fluctuation) followed by rapid change is more widely applicable.

Other intrinsic limitations of Kellogg's study preclude any proof of her preference for phyletic gradualism directed by natural selection. First of all, she has no control on geographic variation. Gradualism cannot be verified in local sections of widely-dispersed species. As Newell argued long ago (1956), spurious "phyletic change" may arise in local sections by successive immigration of normal geographic variants responding to changing local
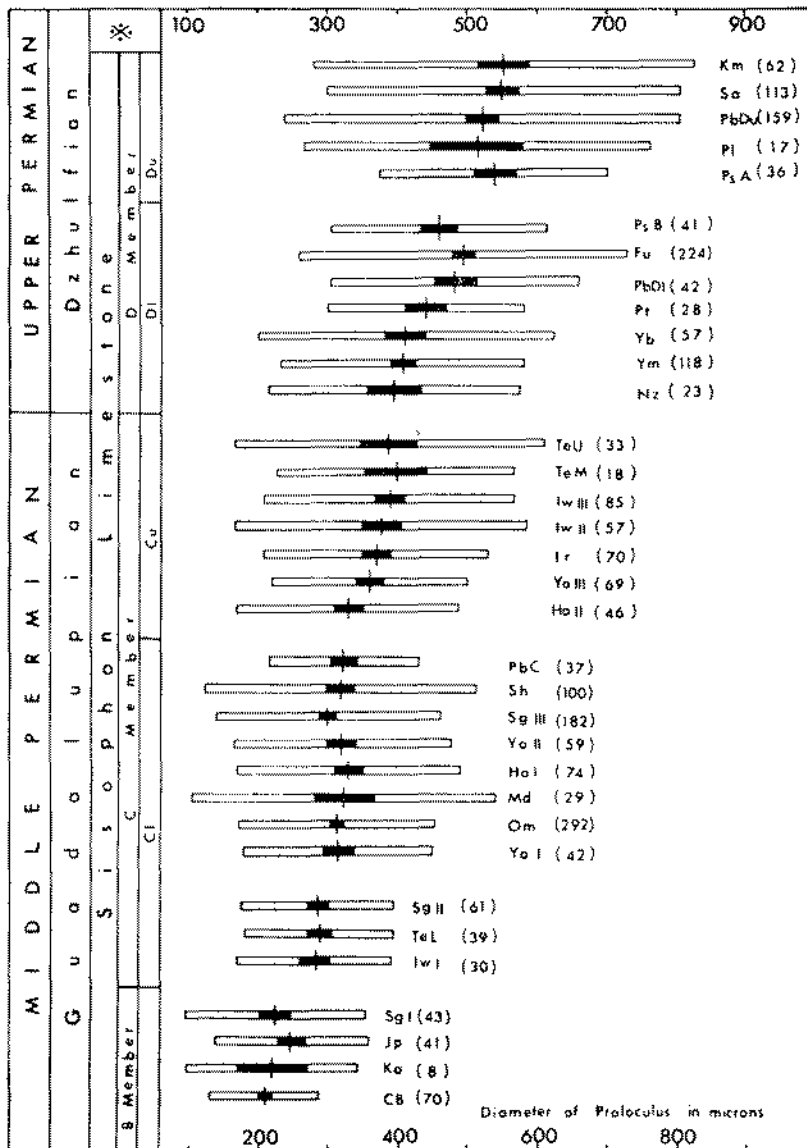
FIGURE 4. Geographic and temporal variation in prolocular diameter for the Permian foraminifer *Lepidolina multiseptata* in East Asia; from Ozawa 1975. Black rectangles are 95% confidence limits for the mean; white rectangles span two standard deviations. Samples grouped together between wider intervals are, in Ozawa's words, "not of successional occurrence but of almost the same horizon"—hence, they represent the rather narrow range of geographic variation for any one time over wide areas. The mean changes by more than 100% during this phyletic sequence.

environments. Take, for example, a mammal distributed through its range according to Bergmann's rule, with larger animals in colder climates. As a local area cools gradually through time, increasing size up section may record nothing more than the shift to lower latitudes of a static range of geographic variation. Many local "trends" in Pleistocene mammals can be explained in this manner. Kellogg proposes that *P. vema* increased in width as waters became colder (1975, p. 361); her "trend" could reflect migration rather than phyletic change. And if the increase is phyletic (affecting the entire species, though only sampled in one spot), why must we invoke genetic change mediated by natural se-

lection—as Kellogg does (p. 368). For basic dimensions of simple creatures, a purely phenotypic response of an unaltered genotype to changing environments seems just as likely. We must not make up stories about the power of natural selection, just because modern theory favors it as an evolutionary agent. In so doing, we do not strengthen the Darwinian cause, but only display our biases. Finally, Kellogg states that she chose *P. vema* (1975, p. 362) because she had noted considerable change of form between its first and last appearance. Unbiased tests of gradualism must study all adequately preserved species in faunas, not only the ones that appear to change. Stasis is data.

2. *Ozawa's forams.* Ozawa's superb study of the Permian verbeekinoid foraminifer *Lepidolina multiseptata* should stand as a model for the testing of evolutionary tempos and the inference of modes. It represents the only case of gradualism that we find fully satisfactory. Ozawa studied 9 characters. Five do not display gradualism; of the four that do, only the change in prolocular diameter is impressive—but it is very impressive (Fig. 4), for a suite of reasons:

i) Samples are sufficiently numerous to preclude any claim of random change. Raup (in press) has shown that this sequence of 34 samples could not, at any reasonable level of probability, arise by a random walk.

ii) Sample sizes are large enough to establish means and variances with sufficient confidence. Sample size ranges from 8 to 292; only 6 of 34 samples contain fewer than 30 specimens, and only 1 has fewer than 10.

iii) The stratigraphic range is large, spanning Middle to Upper Permian times.

iv) Most importantly (for it successfully overcomes the Achilles Heel of most other claims for gradualism), Ozawa has studied geographic variation explicitly. His samples come from a wide geographic area of Southeast Asia, Southern China and Japan. He has demonstrated that geographic variation is slight compared with the magnitude of mean stratigraphic change.

v) The change in prolocular diameter can be correlated with a shift in habitat from shallow carbonates to deeper clastics. Here enough information is available to defend a selectionist interpretation. The change cannot

be merely migrational since geographic variation has been measured and eliminated. It is too long, extensive and persistent to be random. The correlation with altered habitat and the complexity of morphological change (internal as well as prolocular size) points to some genetic alteration: shifting habitat supplies a reasonable selective pressure.

We are delighted with these results, and believe that they reflect well upon our model. We expect counter cases, especially among predominantly asexual forms (see p. 142). We are, like all honest men, anxious to vindicate the substantive predictions of our model: but we also hope that punctuated equilibria will serve as an organizing device for reorienting the central study of evolutionary tempo—away from a biased consideration of rare cases towards a fair assessment that can resolve some important issues in evolutionary theory. In this case, Ozawa used our model to recognize that adequate tests must include an explicit study of geographic variability.

3. *Gingerich's mammals.* Gingerich (1974, 1976, in press) has been our most forceful and cogent critic. He has attempted to trace the phylogeny of several early Eocene mammals by following their stratigraphic history in Wasatchian strata of the Big Horn Basin in Northern Wyoming. His recent study (1976) includes the condylarth *Haplomylus* and the primate *Pelycodus*, but Gingerich bases most of his claims on the more complex phylogeny of the condylarth *Hyopsodus* (Fig. 5)*. Gingerich uses the logarithm of length × width of the first lower molar as his only criterion for a quantitative phylogeny and a defense of gradualism.

In advocating gradualism as the primary tempo of life's history, Gingerich lays proper stress upon a claim that rates of morphological separation in speciation are basically the same as rates of phyletic transformation within lineages. This is a central point often neglected by defenders of gradualism. No gradualist

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* Gingerich has published two other figures with more samples than the section reproduced in Figure 5—1974, and 1976, p. 13. But the test of punctuated equilibria, as Gingerich agrees, must be based on Fig. 5 (his Fig. 4 of 1976, p. 12)—for only this section orders samples by field evidence of stratigraphic superposition alone. The more detailed sections include samples interpolated by assuming gradualism and ordering samples of *Hyopsodus* accordingly. Gingerich states (1976, pp. 10–11) that "the stratigraphic framework must be set up completely independently of the fossils of interest": he then admits (1976, p. 11) that the sections with interpolations "cannot be cited as evidence for gradual phyletic evolution."
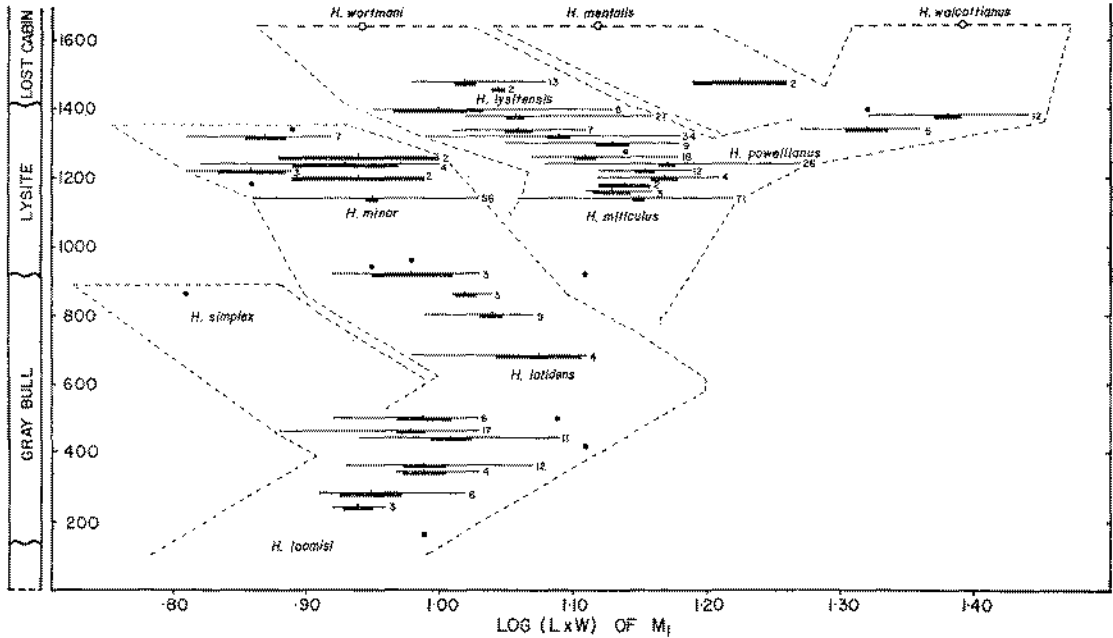
FIGURE 5.   The phylogeny of *Hyopsodus* in the Big Horn Basin as given by Gingerich 1976, and based only on samples in measured sections. Horizontal bar is standard error; horizontal line represents total range of variation; sample size indicated at the right of each distribution; points are single specimens.

can deny that species often arise by splitting—how else could diversity ever increase? It is not enough simply to demonstrate a few cases of gradualism in phyletic transformation; rates of separation between splitting lineages must also be no greater than the average tempo of phyletic change. Gingerich writes (1976, p. 2): "If rates of divergence are relatively slow, that is, as slow as documented rates of phyletic evolution, the diversification of life is properly viewed as a gradual process, species are dynamic links in a great chain, and the traditional branching tree is an adequate representation."

We welcome Gingerich's approach to testing by meticulous stratigraphic work; his data are among the most important ever collected by paleontologists for the study of evolutionary rates. Nonetheless, we cannot agree that his information, as presented, confirms a wide-ranging claim for gradualism; his data on the splitting of lineages seem to fit our model of punctuated equilibria better.   We proceed by three levels of argument:

i) the data, as given, are inadequate in principle to validate gradualism even when the pattern of Fig. 5 seems to indicate unidirectional change;

ii) the pattern of Fig. 5 does not, in fact, establish the prevalence of such unidirectional change;

iii) even if the pattern of Fig. 5 did indicate gradualism, the inferred rates are too slow to account for anything important in evolution.

i) Gingerich presents no study of geographic variation. Gradualism throughout a species of broad range cannot be inferred from local sections. Gingerich determines only what happened in one place—the Big Horn Basin of Wyoming—though he admits (1976, p. 5) that there is "no reason to think that the Paleocene and Eocene faunas of the Big Horn Basin were geographically isolated from their counterparts preserved in other basins in the Rocky Mountains." Gingerich's most impressive evidence for sustained unidirectionality is particularly subject to an alternate interpretation based on migration and an unaltered pattern of geographic variation with no shift of mean values through time. In Lower Gray Bull strata, all three lineages (*Hyopsodus, Haplomylus,* and *Pelycodus*) display a sustained, simultaneous increase in size. Such impressive coincidence leads us to wonder whether Gingerich's notion of similar response

to independent regimes of selection provides the most likely explanation. An alternate hypothesis based on geographic variability is at least as likely: all species vary as Bergmann's rule with larger animals in more northerly latitudes; climate became colder in the Big Horn basin during Graybullian times and larger bodied, northern populations, moved into Wyoming. We do not assert this alternative as intrinsically preferable; we merely point out that Gingerich does not provide the essential data to test it. Any judgment about gradualism requires a knowledge of how *Hyopsodus* changed in other basins.

ii) We do not see the same unambiguous evidence for gradualism that Gingerich affirms in Fig. 5—for several reasons:

a) The dotted guidelines that Gingerich draws about his data are gradualistic interpretations, not literal renderings of the evidence. We find long segments of apparent stasis within supposedly gradualistic sequences. Consider, for example, levels 160–500, a period of supposed size increase leading from *H. loomisi* to *H. latidens*. If we take all nine samples (excluding only the single specimen at level 500 because it is morphologically separate from another sample of six specimens from the same level), and plot them against stratigraphic level, we compute a slope insignificantly different from zero. We are especially grateful to Dr. Gingerich for supplying us with his raw data, knowing full well that we would attempt to use it against him.

$$Y = .9606 + .0001899X$$

Secondly, the *H. miticulus* to *H. lysitensis* lineage supposedly displays gradual size decrease. Indeed, it does to our satisfaction at upper levels; but the first 9 of its 15 samples (spanning 50% of its stratigraphic range) yield a slope insignificantly different from zero, and a decrease (calculated from the curve) from 1.15 to 1.14 in log ($l \times w$) over the entire sequence (Fig. 6).

$$Y = 1.1515 - 0.000092X$$

(We omit from this calculation only the single specimen at level 920, disjunctly situated 220 ft below the initiation of a lineage that only endured for 340 ft over its 15 samples.)

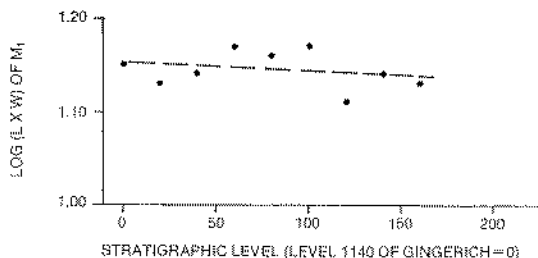b) The major episode of apparent gradualism within *Hyopsodus* (*H. loomisi*—*H.*

FIGURE 6. Plots of mean tooth size versus stratigraphic level for a segment of Gingerich's *Hyopsodus* lineage, as discussed and defined in the text. The regression indicates stasis during a period of supposed size decrease in the *H. miticulus* to *H. lysitensis* lineage. Dotted line is the least squares regression calculated from Gingerich's data.

latidens—*H. minor*) is not a unidirectional trend, but a zigzag of intermediate increase ending up just about were it started (see Fig. 5).

c) We see no evidence for Gingerich's most important contention: that speciation is a process of gradual divergence at rates similar to those in phyletic sequences. Consider *all* cladogenetic events in Fig. 5: *H. simplex* is a single specimen and we can say nothing about it. *H. miticulus* (again omitting the single specimen at level 920) arises disjunctly at a maximal distance from its ancestor, and then evolves in parallel with it. The ratio of means for the two lineages in 1.21 (1.15/0.95) at the inception of *H. miticulus* (level 1140) and 1.25 (1.09/0.87) and 1.19 (1.06/0.89) at their last two sympatric occurrences. *H. mentalis* has only one sample in the Big Horn Basin. Finally, *H. powellianus* includes only three samples, displaying no trend (the first and last samples have the same mean value, though Gingerich's guide lines indicate size increase). Cladogenetic events in *Pelycodus* tell the same tale (there are no such events in the third, *Haplomylus* lineage). Gingerich places special emphasis upon the supposed gradual divergence of "*N.*" *nunienus* from "*N.*" *venticolis* (see Fig. 7; these species are now placed in *Notharctus*, but will be revised by Gingerich): "The two species, once established sympatrically, diverge in a regular way from each other" (1976, p. 25). We admit the gradual size decrease of "*N.*" *nunienus*, but see no evidence for the key claim of gradual departure in sympatry from "*N.*" *venticolis*. Gingerich has only three samples of "*N.*" *venti-*
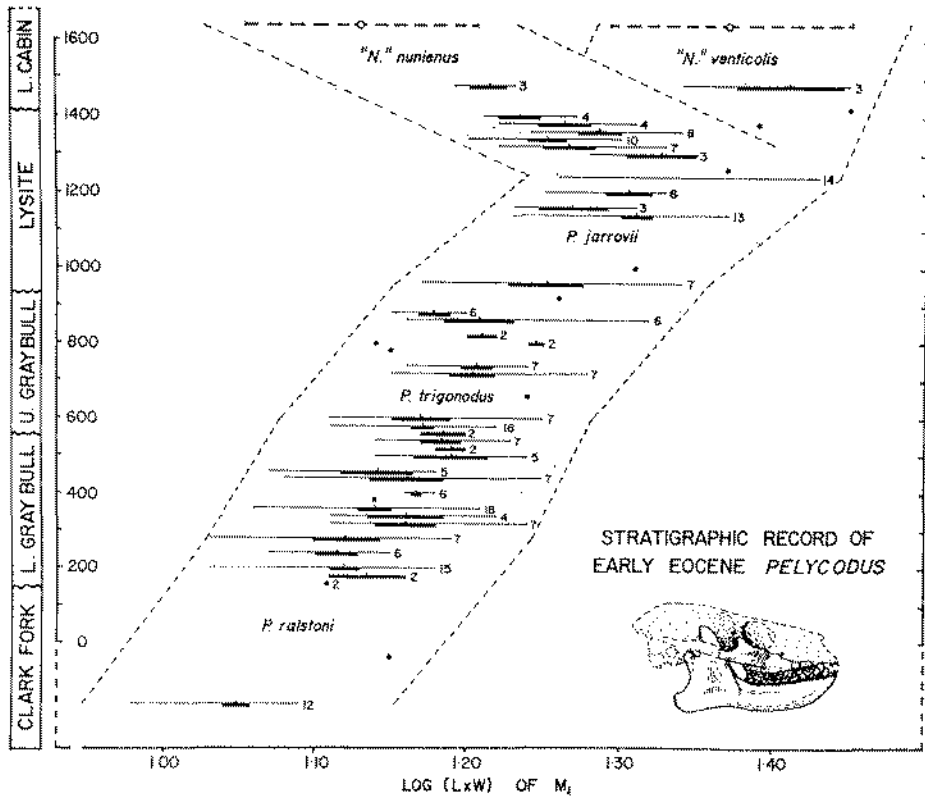
FIGURE 7. Supposedly gradual cladogenesis in the *Pelycodus* lineage, according to Gingerich 1976. Symbols as in Fig. 5. We see no evidence for gradual divergence of "*N.*" *venticolis* from its ancestor.

colis; the first two are based on single specimens, and the literal pattern among the three is a zig-zag of increase followed by decrease. In short, Gingerich presents no evidence for his most important claim that "the paired descendant species appearing after speciation events . . . were not initially distinctive, but only became so after a significant period of time" (1976, p. 25). A literal interpretation of his cladogenetic events would support our model of punctuated equilibria.

d) On a positive note, Gingerich's data for *Hyopsodus* offer the finest confirmation now available for the most important implication of punctuated equilibria (see section IV)—the explanation for trends that we chose not to christen explicitly (Eldredge and Gould 1972, pp. 111–113), and that Stanley (1975) has since called "species selection"—i.e., macroevolutionary trends are not a result of gradualistic orthoselection, but arise from a "higher level selection" of certain morphologies from a random pool of speciation events produced by punctuated equilibria. Species selection depends upon the validity of "Wright's rule" (Gould, in press)—the claim that speciation is essentially random with respect to the direction of a macroevolutionary trend (Wright 1967). Wright's rule must be tested extensively and affirmed if species selection is as fundamental a process as we believe. Gingerich provides the first adequate test. The general trend in the entire *Hyopsodus* clade is towards larger size (all three final species are larger than ancestral *H. loomisi*). Gingerich writes (1974, p. 108): "The *Hyopsodus* radiation clearly conforms to Cope's rule." Yet of the nine species descended from *H. loomisi* on Fig. 5, five evolve towards smaller size, and only four (*H. latidens, H. miticulus, H. powellianus,* and *H. walcottianus*) become larger. We cannot attribute size increase to gradualism within lineages, for not a single lineage displays it (contrary to Gingerich's

TABLE 2. Rates of evolution (assuming gradualism) for Gingerich's most rapid evolutionary events.

Event	Stratigraphic interval (ft)	Inferred time (m.y.)	Log (L × W) beginning and end	L × W beginning and end	√L × W beginning and end	% change (absolute difference between beginning and end divided by beginning value)	% change per million years
A—decrease H. latidens–H. minor	640	1.60	1.08–0.87	12.02–7.41	3.467–2.723	21.5	13.4
B—decrease H. miticulus–H. lysitensis	180	.45	1.13–1.02	13.49–10.47	3.673–3.236	11.9	26.4
C—increase in Haplomylus	660	1.65	0.75–0.83	5.62–6.76	2.371–2.600	9.5	5.8
D—increase in Pelycodus	1140	2.85	1.11–1.33	12.88–21.83	3.589–4.624	28.8	10.1

guidelines, there is no increase within *H. loomisi*—see p. 131). The increase must occur in cladogenesis, and we have already argued that cladistic events conform to punctuated equilibria. The phylogeny of *Hyopsodus* therefore affirms Wright's rule. Size increase in the entire clade arises from the differential success of larger species in a random subset of cladistic events. (In fact, new species are more often smaller than larger.)

iii) Quite apart from the bickering that will continue for years over whether this or that case really exhibits gradualism, we must consider the characteristic rates of supposed gradualistic events. When this is done, one cardinal fact emerges: they are too slow to account for most important evolutionary phenomena, particularly for adaptive radiations and the origin of new morphological designs. We regard gradualism as unimportant in evolution not only because it occurs rarely, but also because its rates are only sufficient to cast a superficial molding upon the pattern of evolutionary change. As Stanley writes (1975): "Phyletic evolution is much more sluggish and less significant than has generally been recognized."

Let us give Gingerich the benefit of all doubt and choose the most rapid rates according to his phyletic interpretations (Table 2). (Gingerich gives three slightly differing estimates of sedimentary rates—20 ft in 45,000, 50,000 or 60,000 yr. We use the intermediate value of 50,000 though any of the three would support our interpretation. We also present Gingerich's rates in the traditional dimension

of length, rather than in his calculation of log length[2] [length × width of molars]; thus, we work with the square root of the antilog of mean values presented in Gingerich's papers).

a) Size decrease in *H. latidens* to *H. minor* (from the first *latidens* at level 680 to the last good sample of *minor* at level 1320—neglecting for Gingerich's sake the single specimen of larger size at level 1340). In 640 ft of section (1.6 m.y.), length decreases by 21.5%, for a rate of 13.4% per million years.

b) Size decrease from *H. miticulus* to *H. lysitensis* (neglecting, for Gingerich's sake, the segment of stasis within the *miticulus* lineage (see p. 131). In 180 ft of section (450,000 yr), size decreases by 11.9%, for a rate of 26.4% per million years.

c) Size increase within *Haplomylus* (Gingerich 1976, p. 15, neglecting the Clarkforkian specimens collected elsewhere and the single specimen at the top of the sequence). In 660 ft of section (1.65 m.y.), we calculate a 9.5% increase in length, for a rate of 5.8% per million years.

d) Since increase within *Pelycodus* (Gingerich 1976, p. 16, again neglecting the Clarkforkian sample collected elsewhere and running to the sample at level 1300, since decrease in size begins immediately thereafter). In 1140 ft of section (2.85 m.y.), length increased by 28.8%, for a rate of 10.1% per million years.

Rates for simple increase in size (without any complex alteration in shape) of 6 to 26% per million years will not encompass the early Tertiary radiation of mammals. We again give Gingerich the benefit of all doubt by using a

"compound interest" rather than an additive model; still, at the most rapid rate of 26% (twice that of any other calculation), a doubling of length still requires 3 m.y. At the average rate of 13.9%, it requires 5.3 m.y. In this particular case, all of Gingerich's lineages originated abruptly in basal Clarkforkian times before the deposition of his Big Horn sequence. These originations fit our model of punctuated equilibria by rapid events of speciation—and they involve fundamental alterations in morphology, not simple change in size. Even if we claim that these lineages arose phyletically in areas not yet explored or devoid of appropriate strata (as Gingerich, in press, speculates), rates must have been many times higher than those calculated in the Big Horn Basin. Gingerich's "trends" seem to be minor fluctuations in the history of lineages that arose abruptly not much earlier.

How can we view a steady progression yielding a 10% increase in a million years as anything but a meaningless abstraction? Can this varied world of ours possibly impose such minute selection pressures so uninterruptedly for so long? The earth's surface is not like the calculating pad of a population geneticist. Lande (1976) has used three of Gingerich's *Hyopsodus* sequences to calcuate selective rates in paleontological events. The minimum amount of selection required to explain these rates is only 1 selective death per 100,000 individuals per generation, corresponding to a truncation point 4.3 standard deviations from the mean. In a burst of understatement, Lande writes: "this is very weak selection." In fact, it is so weak that the change could easily be accomplished by genetic drift, even in large populations (the smallest population size for which such change could occur by drift at least 5% of the time is only 10,000).

The scale of these events is simply all wrong for the usual interpretations extrapolated up from observations made by neontologists in ecological time. Thus, Gingerich (1976, p. 26) would attribute the gradual divergence of two species in sympatry to competition for resources (though in another place, 1974, p. 108, he seems to be aware that his rates are too slow): "Both the differing deme and its homogeneous neighbors might survive, each creating a strong (sic) directional field of selection. . . . A parent species divided into two new sister species which subsequently diverged to minimize competition with each other." Not at a rate of 10% change in length per million years! For such a rate is invisible in ecological time. Character displacement is a geologically instantaneous process (see Eldredge 1975).

If such tiny, sustained rates of change actually exist in paleontological time, what do they mean? Traditionally, they have been interpreted as the primary defenders of conventional selection theory. But we demur, for the rates are far too slow and far too continuous for selection in such a dynamic world. We wish cautiously to float a radical proposal: perhaps these rates do not provide a comfortable confirmation of traditional panselectionism; perhaps they constitute a fundamental mystery worthy of our serious thought and attention.

E) *Cases that confirm punctuated equilibria.* —By emphasizing cases presented as contrary to our model, we do not wish to imply that we are without supporters. In fact, most published commentary on punctuated equilibria has been favorable. We are especially pleased that several paleontologists now state with pride and biological confidence a conclusion that had previously been simply embarrassing ("all these years of work and I haven't found any evolution").

Several lineages have been cited in support of our model. Kellogg and Hays (1975) argue that about 1.9 m.y. ago, a small population of the radiolarian *Eucyrtidium calvertense* invaded subarctic waters north of the Arctic Convergence. There it evolved rapidly and allopatrically to *E. matuyamai*, a larger and more robust species. *E. matuyamai* then invaded the range of its ancestor. For the previous two m.y., *E. calvertense* had been stable in size, but it decreased rapidly after contact with its larger descendant. When *E. matuyamai* became extinct a short while later, the evolution of *E. calvertense* to smaller size ceased.

Reyment (1975) presents an interesting case of "pseudo-gradualism," resolved to abrupt disjunction by the study of covariance rather than static adult morphology. In upper Turonian strata on Hokkaido, the "generic" transition from *Subprionocyclus normalis* to *Reedsites minimus* is clearly continuous in basic dimensions of adult morphology. Means and

covariances are so similar that the first four eigenvectors of principal components for each species taken separately are virtually identical. But the pattern of covariance between these variables and measures of ornamentation changes abruptly. Correlation coefficients between ornamentational and dimensional variables range $+.39$ to $+.55$ in *R. minimus* and from $-.32$ to $-.50$ in *S. normalis*. Reyment concludes (1975, p. 675):

> The major morphological difference between the two genera did not take place gradually. . . . The change was not heralded by a gradual change in the frequencies of the ornamentational characters. . . . The concept of 'punctuated equilibria' of Eldredge and Gould seems to fit these observations well.

Other paleontologists have presented patterns in larger clades as affirmations of our model. Henry and Clarkson (1975) discerned a clear trend to greater complexity of enrollment structures in the Ordovician trilobite *Placoparia*. But they detect no gradual change within any species, while patterns of geographic variation point to the prevalence of allopatric speciation. The trend seems to be a result of species selection.

In his study of Arenigian olenid trilobites in Spitsbergen, Fortey has followed both our primary recommendations for a reformulation of method in the study of evolutionary tempos —study all taxa, and consider stasis as data. Fortey (1974) collected bed by bed through an "exceptionally complete record" (1974, p. 4) and established the phylogeny of an extensive adaptive radiation in the Balnibarbiinae. He concludes that "the period of derivation of a new species from its ancestor is short compared with its subsequent duration, and that this speciation pattern is consistent with the allopatric model" (1974, p. 4). Fortey rejects the attribution of morphological gaps to breaks in the stratigraphic record because times of origin do not correspond in different lineages and because he finds no lithological indication of non-sequence or even of reduced sedimentation at points of origination for new species. Fortey concludes, in confirmation of traditional stratigraphic practice (1974, p. 20): "Evolution in this case defines discrete morphological groups with a particular stratigraphic range—that is, that paleontological

species seem to have real meaning among these olenids rather than being arbitrary points on a continuous morphological spectrum changing with time."

We are particularly pleased that our model of punctuated equilibria has been used to reassess the evolution of the clade most near to all our hearts—the peculiar pongid offshoot whose only living representative is *H. sapiens* (see Walker 1975; and Pilbeam 1975). In no other group, has the a priori assumption of gradualism been so pervasive. It supported racial classifications to justify imperialism in the nineteenth century, and it still regulates our exalted view of our own estate. The bias is so strong that Brace (1967) once labelled as "hominid catastrophism"—a rearguard action of those who still do not wish to accept our brutish ancestry—all attempts to deny direct ancestral-descendant relationships among known hominid fossils, and to attribute observed patterns to extinction and subsequent migration. Human evolution has been viewed as a ladder of progress.

Recent discoveries have discredited the naive notion of a single lineage, *Australopithecus africanus—Homo erectus—Homo sapiens*, with gradual increase in brain size within each taxon. All new evidence points to a branching bush with rapid origination and subsequent stasis within taxa (Eldredge and Tattersall 1975; Gould 1976). On mechanical and biometric grounds, Oxnard (1975) has argued that the australopithecines, although a sister group to us, were not directly ancestral to any subsequent hominid. (Several paleoanthropologists who generally support our model do not accept Oxnard's specific conclusion—E. Delson and A. Walker, for example). In any case, there is no direct evidence for gradualism *within* any hominid taxon—*A. africanus*, *A. robustus*, *A. boisei*, *H. habilis*, *H. erectus*, and even *H. sapiens*. Each species disappears looking much as it did at its origin; admittedly "progressive" trends result from the differential survival of discrete taxa.

Richard Leakey's discovery of hominid E.R. 1470 has shattered the conventional view that *Homo* evolved gradually from *A. africanus*; for this member of our genus, with its cranial capacity of nearly 800 cc, lived in sympatry with australopithecines, perhaps as long as 3 m.y. ago. The more recent discovery of a remarkable *H. erectus* from the Koobi Fora

Formation, east of Lake Turkana in East Africa has discredited the strongest traditional tale of hominid gradualism—a progressive increase in brain size from primitive demes in Java to the advanced population at Choukoutien (Peking Man). This specimen, older than any non-African *H. erectus*, has a cranial capacity "well within the range of the Peking specimens" (Leakey and Walker 1976, p. 572). (See Howells, in press, for a defense of *H. erectus* as a stable taxon, not a grade in a tale of continuous improvement.)

Finally, several paleontologists have supported our model for broader patterns in the major groups of their expertise. These qualitative assessments follow our criterion of relative frequency. After a major study of Middle Cambrian agnostid trilobites in western North America, Robison (1975) concludes: "I have found a conspicuous lack of intergradation in species-specific characters, and I have also found little or no change in these characters throughout the observed stratigraphic ranges of most species" (1975, p. 220). "Most species of the suborder Agnostina are non-intergrading and best fit an allopatric model of speciation" (1975, p. 219).

Johnson (1975) has assessed the relative frequency of evolution by allopatric speciation in Devonian brachiopods and has come down strongly on our side, primarily because most variation within species is geographically rather than temporally distributed. Johnson reached this conclusion only after years of search for preferred examples of phyletic gradualism. Recalling the hope engendered by gradualism in *Eocoelia* (Ziegler 1966), he writes (1975, p. 657):

> After completion of Ziegler's paper we talked a number of times about the possibilities for duplicating his efforts with other fossils and in other times. It was a heady prospect. . . . In subsequent years many workers have attempted to seek out and define lineages of brachiopod species and other megafossils in the lower and middle Paleozoic with little success. My conclusion, subjective in many ways, is that speciation of brachiopods in the mid-Paleozoic via a phyletic mode has been rare. Rather, it is probable that most new brachiopod species of this age originated by allopatric speciation.

Ager (1973, 1976) shares the same view for Mesozoic brachiopods: "In twenty years work on the Mesozoic Brachiopods, I have found plenty of relationships, but few if any evolving lineages. . . . What it seems to mean is that evolution did not normally proceed by a process of gradual change of one species into another over long periods of time. I have long criticized the notion that evolution can be studied by chasing fossil oysters up a single cliff. . . . One must clearly study the variation of a species throughout its geographical range, at one moment in geological time, before one can claim that it has changed into something else" (1973, p. 20).

Reyment (1975) has supported stasis as a predominant tempo, even for microorganisms from continuous sections—the usual arena of greatest hope for abundant gradualism: "The occurrences of long sequences within species are common in boreholes and it is possible to exploit the statistical properties of such sequences in detailed biostratigraphy. It is noteworthy that gradual, directed transitions from one species to another do not seem to exist in borehole samples of microorganisms" (1975, p. 665). MacGillavry (1968, p. 70) was also forced by his own observations to abandon a previous commitment to gradualism for microorganisms in local sections: "During my work as an oil paleontologist I had the opportunity to study sections meeting these rigid requirements. As an ardent student of evolution, moreover, I was continually on the watch for evidence of evolutionary change. . . . The great majority of species do not show any appreciable evolutionary change at all. These species appear in the section (first occurrence) without obvious ancestors in underlying beds, are stable once established, and disappear higher up without leaving any descendants." We do not cite these two statements about local sections as documentation of our model, for we have emphasized that the study of geographic variation is an indispensable component of any decision. These statements do, however, confute the basic tenet of gradualism that even transition pervades entire populations.

In summary, our model has survived its first five years in excellent shape. It has received much empirical support and has fit the impression of many specialists who spent a professional lifetime searching for gradual-

ism within their groups. It is very hard to find probable cases of gradualism, even in geologically optimal situations; most reported cases resolve to little more than wishful thinking. Moreover, all these tests are based on a biased selection of cases known to exhibit some evolutionary change. What would happen if paleontologists carried out large-scale, unbiased studies that admitted stasis as data and considered all taxa in a fauna? We cannot avoid the prediction that punctuated equilibria would assume even greater importance.

F) *A note on indirect tests from the genetics of living organisms.*—Punctuated equilibria needs one "enabling criterion" from the genetics of speciation in living organisms. We must be able to assert that a major amount of genetic change often accumulates in the event of speciation itself. If nearly every case of recent speciation separated a daughter population only minutely from its parent, and if greater genetic divergence were primarily a function of time, then gradualism would receive some support. We must be able to state that Mayr's "genetic revolution" (Mayr 1963, p. 538) is a common component of speciation. (As Stanley [1975] emphasizes, it need not be a ubiquitous property. Indeed, since speciation is defined only as the acquisition of reproductive isolation, it must often occur with only minor genetic input—as when, for example, small genetic changes produce a shift to a new host plant in host-specific insects—Bush 1969.)

Mayr supported his notion with indirect evidence of external morphology; recent research in biochemical genetics has confirmed his suspicions. Ayala et al. (1974) studied the genetics of speciation in the *Drosophila willistoni* group. They found that a substantial amount of genetic differentiation (averaging .23 electrophoretically detectable allelic substitutions per locus) occurred during what they called the "first stage" of speciation—i.e., in allopatric, isolated populations that have already acquired at least partial reproductive isolation. Sister species in the "second stage" (now in sympatry and completing reproductive isolation) differed no more than pairs still in the first stage. Avise (1976) has generalized these conclusions. He finds that individuals in interacting populations generally share up to 99% of the structural genes surveyed by electrophoresis, while "populations

showing incipient reproductive isolation, often in the form of hybrid sterility, exhibit significantly greater genetic distances, involving major allelic changes at up to 20% or more of structural genes" (1976, p. 113). Again, a major genetic alteration characterizes the early stages of speciation, following spatial isolation and the establishment of (even imperfect) reproductive isolation. Avise concludes (1976, p. 120): "Arguments that speciation is normally accompanied by little genetic change are clearly refuted." The fact that strongly differentiated species exhibit far less genetic similarity speaks neither for nor against our model; for we do not know whether increasing genetic distance results from gradual separation or from the interposition of additional speciation events between the common ancestor and surviving taxa.

A few studies in biochemical genetics speak more directly to our hypothesis. They also speak very ambiguously, some for and some against. In a work that provides evidence against our model, Avise and Ayala (1976) studied average structural-gene differences between species in two clades of fishes, the centrarchid *Lepomis* with 11 living species, all North American, and the North American minnows, with 250 species. Scrappy fossil evidence indicates that both clades are equally ancient (the first *Lepomis* appears at the Miocene-Pliocene border, while the first fossil minnows are Miocene). If both clades are the same age, then their major difference lies in the number of speciation events. By our model, random pairs of minnow species should be more genetically dissimilar than random pairs of *Lepomis* since, on average, they will be separated by more speciation events. Average distances are similar for pairs of species within the two clades.

We applaud this approach to the genetic study of evolutionary divergence, but we do not consider this case as strong evidence against our model—and neither do Avise and Ayala (personal communication). First of all, too many uncertainties envelop the study (as Avise 1976, p. 118, admits). Are the clades really of equal age? Are the selected minnows, all from California, truly a random subset of their clade, or might they represent a subgroup with rather recent times of divergence from each other?

Our second reservation is far more impor-

tant: We do not know what these changes in structural genes represent in terms of adaptive evolution. After years of squabbling and out-of-hand denial, evolutionary biologists must now take seriously the proposition that many, if not most, changes in structural genes drift to fixation in the neutral mode, do not affect phenotypes, and are therefore both irrelevant and invisible to Darwinian processes (e.g. Nei 1975). Neutral substitutions will accumulate in clock-like fashion and lead to the conclusions affirmed by Avise and Ayala in their genetic studies of fishes. But neutral substitutions are irrelevant both to gradualism and to punctuated equilibria, for both deal with adaptive, phenotypic evolution. (A gradualist can take no comfort in the prospect of random genetic divergence, even among genes with phenotypic effects, for this process will yield directional trends in morphology only at the low frequency that stochastic processes allow—see Raup, in press.)

We wish to propose a potential use of our model in molecular genetics. (We cannot advocate it here because we are arguing for the validity of punctuated equilibria, not for schemes that only work by assuming its truth.) If a future consensus judges our model favorably, then it can serve as a test for neutralism, and the information provided by minnows and *Lepomis* would support the hypothesis that most changes in structural genes are neutral. The argument is similar to that advanced by Zuckerkandl (1968). Assuming the validity of von Baer's laws, Zuckerkandl predicted that fetal proteins would be less different than corresponding adult proteins in the same species. But he measured equal levels of divergence. This discovery leads in two opposite directions: either von Baer's laws are wrong and we should not expect greater evolutionary conservatism in fetal than adult structures, or von Baer's laws are valid and the changes are neutral with respect to adaptation. Since von Baer's laws have received overwhelming support for 160 years, Zuckerkandl chooses the second option. He concludes that adaptive evolution occurs primarily by changes in genetic regulation; these are not examined in conventional studies of genetic distance based upon structural genes alone: "Reproducible morphogenesis depends on constancy of genic regulation to a larger
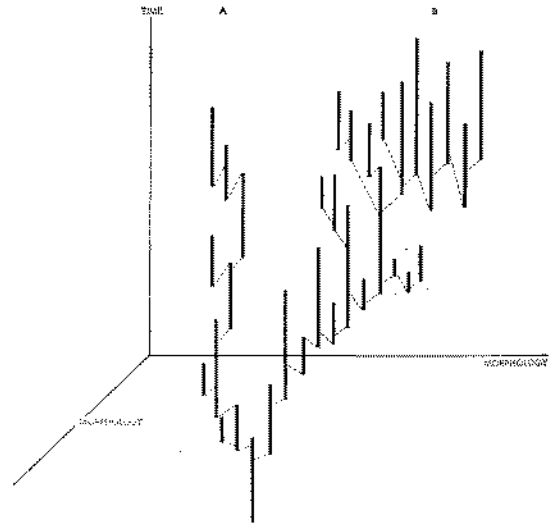

FIGURE 8. The origin of an evolutionary trend by species selection, rather than directed gradualism. From Eldredge and Gould 1972. Stasis prevails within species, and speciation is random with respect to the direction of the evolutionary trend.

extent than on constancy of genic structure" (Zuckerkandl 1968, p. 270).

We applaud the burgeoning emphasis on change in regulatory genes as the stuff of morphological evolution (Wilson 1976; King and Wilson 1975; Valentine and Campbell 1975), if only because one of us has written a book to argue that the classical, and widely ignored, data on evolution by heterochrony should be exhumed and valued as a primary demonstration of regulatory change (Gould 1977). We do not see how point mutations in structural genes can lead, even by gradual accumulation, to new morphological designs. Regulatory changes in the timing of complex ontogenetic programs seem far more promising—and potentially rapid, in conformity with our punctuational predilections. The near identity of humans and chimps for structural genes (King and Wilson 1975), and the evidence of major regulatory change indicated by human neoteny (Gould 1977) provides an important confirmation.

We are pleased that some recent molecular evidence, based on regulatory rather than structural gene changes, supports our model. Ferris and Whitt (1975) have studied the evolution of diploidization in catostomid fishes. They regard the ancestor of their clade as tetraploid. More specialized modern genera

owe their status to a greater number of intervening speciations between common ancestor and living fish (Ferris, talk at A.I.B.S., New Orleans, 1976). Unspecialized genera are equally old, but are separated by fewer speciations from the common ancestor. If the Avise-Ayala conclusion for structural genes were to apply, we would expect an equal amount of diploidization in specialized and unspecialized genera. But Ferris and Whitt (1975, p. 30) find a positive correlation between this change in regulation and the number of speciation events: "We conclude that a slow return to a diploid level of gene expression is occurring in all genera, but that this diploidization occurs more rapidly in the more specialized genera. This may be attributed to the progressive loss or inactivation of some duplicated loci."

IV. Punctuated Equilibria as the Basis for a Theory of Macroevolution: The Speciation Theory

When we were writing our initial paper, no conclusion excited us more than the insight offered by punctuated equilibria for a new interpretation of evolutionary trends. We argued that evolutionary trends did not usually arise by orthoselection in gradually-changing lineages, but that they represented the differential success of subsets from a potentially random pool of speciation events (Fig. 8, reproduced from our 1972 paper). In this perspective, speciation is the raw material of macroevolution, and genetic substitution within populations cannot be simply extrapolated to encompass all events in the history of life. We therefore challenged the central assumption that secured the admission of paleontology into the modern synthesis of evolutionary theory (Simpson 1944 and 1953): change in gene frequency within populations is the building block of major evolutionary events. We wrote (1972, p. 112):

A reconciliation of allopatric speciation with long-term trends can be formulated along the following lines: we envision multiple 'explorations' or 'experimentations' (see Schaeffer 1965)—i.e. invasions, on a stochastic basis, of new environments by peripheral isolates. There is nothing inherently directional about these invasions. However, a subset of these new environments might, in the context of inherited genetic constitution in the ancestral components of a lineage, lead to new and improved efficiency. Improvement would be consistently greater within this hypothetical subset of local conditions that a population might invade. The overall effect would then be one of net, apparently directional change: but, as with the case of selection upon mutations, the initial variations would be stochastic with respect to this change. We postulate no 'new' type of selection.

We declined to designate with a new name this phenomenon of macroevolution by differential success of speciation events because we regard it as so fundamentally consistent with basic Darwinism. It represents no departure from Darwinian mechanisms, but only the previously unrecognized mode of operation for natural selection at hierarchical levels higher than the local population. Surely, the extinction and persistence of species is as Darwinian an event as the spread of genes through populations. The differing geometry of change is simply an "allometric" phenomenon of scale: the same process works in differing ways at different levels of complexity and organization. Stanley (1975a) has since designated this process as "species selection." We were inclined, at first, to reject this special name (Gould, in press), since it carries the unfortunate implication of a novel mechanism inconsistent with natural selection—while we believe that "species selection" represents no more than the operation of natural selection at higher levels. Nonetheless, recognizing a peculiarity of human psychology—that the importance of a phenomenon is not recognized unless it has a special name—we drop our objection, while reiterating our hope that the relationship of species selection to Darwinian theory will not be misconstrued.

Species selection follows directly from the validity of two premises; these must first be tested and affirmed if species selection is to form the basis for a theory of macroevolution:

i) the model of punctuated equilibria itself;

ii) the proposition that a set of morphologies produced by speciation events is essentially random with respect to the direction of evolutionary trends within a clade. Sewall Wright (1967) made this suggestion in explicit analogy with the lower-level phenomena of random mutation and natural selection within

populations. We suggest that this proposition be termed "Wright's rule,"* and that its testing be an item of high priority in paleobiology. We have already showed (pp. 132–133) that Gingerich's phylogeny of *Hyopsodus* provides a first, impressive confirmation.

Wright's analogy represents the key to a claim that a new theory of macroevolution lies in the expression: punctuated equilibria + Wright's rule = species selection. Let us simply call it the "speciation theory" of macroevolution. Previously, mutation and natural selection within populations were regarded as fully sufficient to render macroevolution: one had only to extrapolate their action directly to longer times and higher taxa in larger clades. But if we (1972) and Stanley (1975a) are right, then speciation interposes itself as an intermediate level between macroevolutionary trends and evolutionary events within populations. Species become the raw material of macroevolution: they play the same role, at their level, as mutations do in local populations. All movement from micro to macroevolution must be translated through the level of species by Wright's grand analogy, not merely extrapolated up in continuity. As Stanley puts it so well (1975a, p. 648):

> Macroevolution is decoupled from microevolution, and we must envision the process governing its course as being analogous to natural selection but operating at a higher level of organization. [We would say that it *is* natural selection, working at a level higher than the local population.] In this higher-level process species become analogous to individuals, and speciation replaces reproduction. The random aspects of speciation take the

place of mutation. Whereas, natural selection operates upon individuals within populations, a process that can be termed species selection operates upon species within higher taxa, determining statistical trends.

If the speciation theory of macroevolution is of general interest, it should perform as all good theories to resolve paradoxes, reinterpret old observations, and synthesize under a common rubric phenomena previously uncoordinated. To cite just four examples of its potential application:

1. Stanley (1975b) has developed an elegant proposal to resolve, at least in part, the classicial paradox of why so inefficient a system as sexual reproduction appears so commonly in nature. Traditional arguments focus on *immediate* adaptive benefits to the sexual organisms themselves: sex accelerates evolution by providing efficient genetic recombination or by permitting the rapid spread of useful mutations through populations. But Stanley proposes an equally forceful argument based *retrospectively* on evolutionary history—an eminently paleobiological input to a traditional neontological dilemma. He points out that asexual clones do not speciate easily, while sexual clades more readily divide themselves into separate species because interacting individuals form interbreeding populations that often split into geographically isolated subgroups. Thus, sexual species are not more numerous because sex itself provides strong adaptive advantages. Asexual species are just as successful and abundant by number of individuals. Sexual species predominate simply because they maintain a high capacity for speciation, while asexual clones do not.

2. Gradualism is not the only prior prejudice constraining paleontological thought. A prominent place must also be awarded to our propensity for explaining all questions of diversity and success in terms of morphological adaptation (Eldredge, in press). Consider, for example, the allied opposites of "overspecialization" and "Cope's law of the unspecialized." Extinction, it is said, inevitably overtakes overspecialized taxa because they are narrowly committed, through elaborate and complex morphology, to a very small range of environments. These taxa are almost invariably large in body size, and owe their morphological elaborations, at least in part,

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* We choose Wright's name for our designation because he (1967, p. 121) explicitly suggested that speciation might by truly stochastic with respect to the direction of evolutionary trends. But we wish to record our debt to Ernst Mayr who has so forcefully and consistently supported the idea that speciation is the stuff of evolutionary change. In fact, Mayr (1963, p. 621) also analogized speciation with mutation in the following remarkable passage:

I feel that it is the very process of creating so many species which leads to evolutionary progress. Species, in the sense of evolution, are quite comparable to mutations. . . . It appears then that a prodigious multiplication of species is a prerequisite for evolutionary progress. . . . Speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. Without speciation there would be no diversification of the organic world, no adaptive radiation, and very little evolutionary progress. The species, then, is the keystone of evolution.

We also note that Mayr, with his notion of the "genetic revolution" (1963, pp. 538–541), is the architect of a punctuational view of speciation within modern Neo-Darwinism.

to allometric intensification (Rensch 1960). Small bodied, morphologically unspecialized taxa, on the other hand, serve as the source for almost all major groups because they retain the morphological flexibility to change in many directions. The basic observations are probably true: large, complex forms are ultimately doomed, while small, simple species often proliferate. But we suspect that relative ability to speciate, not morphological flexibility, provides an interpretive key, heretofore unrecognized. Large animals live in small populations and do not fraction easily into isolated subgroups. (Some exceptions to this generality appear among large mammals with complex social systems involving fractionation into family and kin groupings. Bush et al. [in press] explain high rates of speciation among horses in this manner.) Small animals maintain populations large enough to weather severe density-independent mortality, while their limited mobility and coarse-grained perception of the environment permit an easier separation into isolated subgroups. All species, the phenomenally successful as well as the narrowly committed, will succumb in due time unless they leave descendants via speciation. In Wright's grand analogy, speciation = variability; clades and populations are equally doomed without variability.

3. Darlington (1976) would separate macroevolution into small-population events for the rapid production of many species and large-population events for the development of broad and general adaptations. Adaptive radiations begin with the evolution of key adaptations in large populations, followed by their general deployment through speciation in small ones. Darlington writes: "The two parts of evolutionary explosions—the primary adaptations and the secondary radiations—should be clearly distinguished. The first part is probably mainly a large-population process (p. 1363). Large groups evolve more effectively than small ones at the same level" (p. 1362—because "they can put together selectively advantageous events that occur separately, and they can pay relatively heavy, complex costs of adaptation"). All this makes excellent sense under Darlington's "inarticulated major premise" (hidden assumption) of phyletic gradualism. If evolutionary events must occur *within* populations, then we cannot deny his arguments. But his dual scheme reduces to the single phenomenon of ordinary speciation, if general adaptations arise by species selection. The precondition for general adaptation need not be many individuals in a large population; many events of speciation within a clade should serve just as well. Evidence is, to say the least, spotty: but nothing in the fossil record can encourage Darlington's belief that major morphological innovations occur in large, stable, and widespread populations.

Darlington's paper illustrates a belief almost universally held among adherents to the modern synthesis (Rensch 1960; Huxley 1958, for example)—that evolution proceeds in two basic modes: anagenesis, or progressive evolution ("improvements," or general adaptations by phyletic transformation); and cladogenesis, or diversification by splitting. Ayala (1976, p. 18), for example, writes:

> Anagenesis, or phyletic evolution, consists of changes occurring within a given phyletic lineage as time proceeds. The stupendous changes from a primitive form of life some 3 billion years ago to man, or some other modern form of life, are anagenetic evolution. Cladogenesis occurs when a phylogenetic lineage splits into two or more independently evolving lineages. The great diversity of the living world is the result of cladogenetic evolution.

We find intellectually satisfying (though not necessarily true on that account) the reduction of these supposed processes to the single phenomenon of speciation—for, in our model, anagenesis is only accumulated cladogenesis filtered through the directing force of species selection.

4. The speciation theory may help us to predict differences in evolutionary tempos among groups. A higher frequency of gradualism seems to characterize the predominantly asexual protists (though still not very high—see statements of Reyment and MacGillavry, pp. 136). Gradualists would attribute this to a better stratigraphic record and would anticipate its occurrence across all groups. But the best examples of protistan gradualism (e.g., Ozawa 1975) do not come from continuous oceanic cores, but from traditional continental sequences containing, in abundance, other taxa that do not display gradualism.
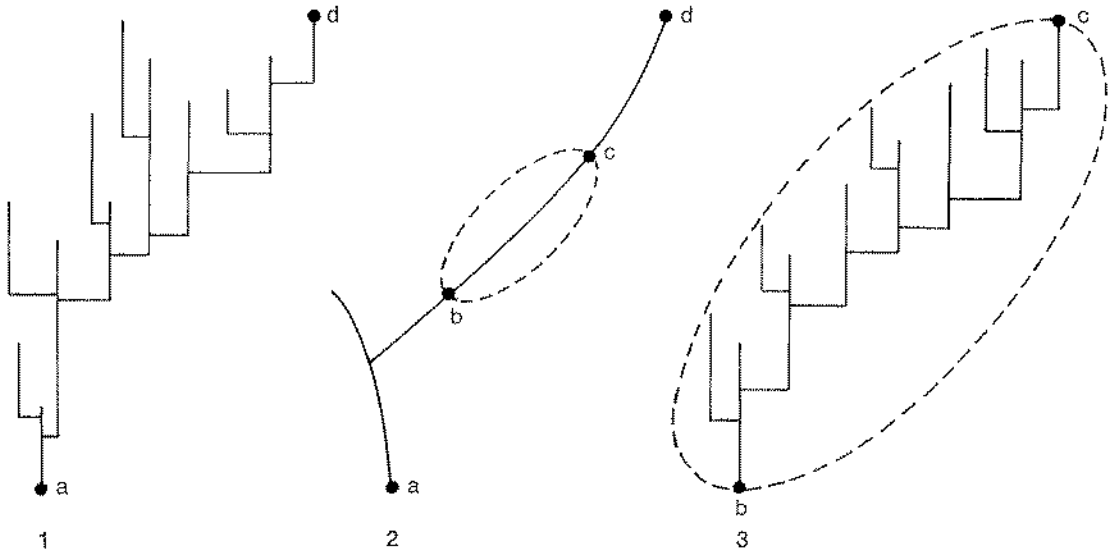
FIGURE 9.   The resolution of apparent gradualism in asexual lineages to punctuational events at the appropriate level of clones. (1.) A trend produced by species selection in a sexually reproducing species. a is an ancestor; d, a descendant. The trend arises only because species with favored traits live longer and branch more often than others. Note stasis within each species and equal number of branching events in each direction. (2.) Apparent gradualism in the branching of a descendant species from its ancestor in asexual organisms; asexual "species" are assemblages of independent clones; these clones, rather than the taxonomist's artificial "species," should be the unit of macroevolution in asexual forms. (3.) Magnification of the apparently gradualistic segment of (2) to show individual clones. These clones follow the punctuational pattern of stasis within and rapid (in this case truly sudden, by definition) change between units. The trend is a result of clone selection; clones with favored traits live longer and branch more frequently. Note stasis within each clone, and equal number of branching events in each direction.

We predict more gradualism in asexual forms on biological grounds. Their history should be, in terms of their own unit, as punctuational as the history of sexual Metazoa. But their unit is a clone, not a species. Their evolutionary mode is probably intermediate between natural selection in populations and species selection in clades: variability arises via new clones produced rapidly (in this case, truly suddenly) by mutation. The phenotypic distribution of these new clones may be random with respect to selection within an asexual lineage (usually termed a "species," but not truly analogous with sexual species composed of interacting individuals). Evolution proceeds by selecting subsets within the group of competing clones. If we could enter the protists' world, we would view this process of "clone selection" as punctuational. But we study their evolution from our own biased perspective of species, and see their gradualism as truly phyletic (Fig. 9)—while it is really the clonal analog of a gradual evolutionary

trend produced by punctuated equilibria and species selection.

We suggest that the "speciation theory of macroevolution" be explored by working through the details of Wright's grand analogy and considering the consequences. Stanley (1975, p. 649) has begun this process, and we extend it here (Tables 3 and 4). No strategy is as slippery and dangerous as analogy. (It may also be true that none is more rewarding; Darwin, after all, constructed the theory of natural selection as an analog to artificial selection by breeders.) Many phenomena at one level have no legitimate correspondent at another; in these respects, the levels are fundamentally different. Recombination, the interaction of individuals within populations, has no common analog at other levels; clones may interact through occasional sexuality and species (at least in some clades) by hybridization, but these are exceptional rather than characteristic processes. Similarly, the programmed course of individual ontogeny has no analog

TABLE 3. Three distinct levels of evolution in the light of Wright's analogy. Starred items do not translate well across levels.

level in organization	sexual species (individuals sharing basic genome and distributing variation by recombination)	asexual "species" (clones sharing basic genome and program of regulation; variation not well distributed by interaction among units)	clade (species sharing a basic adaptive plan)
individual unit of the level	individual organism	clone	species
*individuals interact by	recombination	(limited recombination in occasional sexual events)	(limited hybridization)
*life course of an individual	programmed ontogeny	stasis by definition till extinction (a new mutation forms a new clade)	no inherent direction; stasis or fluctuation probable; gradual change very rare
source of new variability	mutation	formation of new clones by mutation	speciation
relation of variability to the direction of evolution	random by chemical nature of mutation	random by chemical nature of mutation	random if Wright's rule holds
mechanism for differential increase of favorable variation	individual selection (conventional natural selection)	clone selection	species selection

in the history of clones and species; in fact, the overthrow of this analogy was a major accomplishment of evolutionary paleontology—discrediting the theory of racial life cycles.

We believe, however, that the insight far outweighs the danger; the analogy is, at least, a most fertile field for speculation, ten percent of which might be fruitful. Try, for example, to translate the theory of r and K selection from ecological to evolutionary time. Many paleontologists have tried to apply this theory, without great success, especially to periods of mass extinction in the history of life; but they have not translated it properly through the analogy.

Consider successful clades that are both diverse and long-lived. Traditional thought would attribute their abundance and persistence to good morphological design, fashioned and tested in competition against species of other clades. But just as life history parameters of maturation time and reproductive effort have been used to explain "success" in ecological time, so must the macroevolution-

ary analog of speciation rate be included in our study of successful clades (Table 3). A macroevolutionary analog to an r-strategist might be a clade that consistently produces many species—let us call these the increasers; an analog to a K-strategist might be a clade that produces species resistant to extinction, either because they compete well against others, or because they survive diversity-independent mass extinctions—let us call these the survivors. We recognize that the "survivors" include species that are both r and K strategists in ecological time. We are not bothered that a macroevolutionary analog of K selection might be a clade that contains r-selected species, for we have emphasized the fallacy of direct extrapolation between levels. In this case, the key notion to translate through the analogy is rapid production of individuals (species) vs. production of good survivors. If this analogy to r and K selection fails, it will fall because increaser and survivor clades may not exhibit the trade-offs so essential to

TABLE 4.　Determinants of evolutionary success in species and clades.

	Species	Clades
criterion	differential reproductive success of certain genotypes	differential survival of certain species
enhancer of success	abundant genetic variability	many peripheral isolates (or incipient species by another model of speciation)
strategies for success		
rapid rates of increase	high r	high speciation rate (increaser clades)
	by high fecundity	consistently high speciation rate
	by early maturation	preemption of adaptive zone by abundant speciation during early history of a clade
differential persistence	differential survival of favored genotypes	resistance to extinction (survivor clades)
	abundance: high frequency of a gene—to resist density independent mortality	large populations to resist diversity independent extinction
	flexibility: "all purpose" genes conferring physiological or morphological plasticity	large environmental range (law of the unspecialized)
	competitive superiority: success in direct, intra-specific competition (K selected genotypes)	triumph over other species in direct competition (survivors by competition)

the r-K distinction; i.e. the species of increaser clades may also be good survivors.

In any case, we make this distinction to emphasize that traditional arguments of morphological advantage apply only to one subcategory of survivor clades—survivors by competition (Table 4). (We assume that survivors by escape from diversity-independent mass extinction do not owe their rescue to generally superior design but to eurytopy or to life in surviving habitats, etc.) Clades that achieve their success through gradual increase in membership during geologically untroubled times may indeed owe their good fortune to evolutionary trends in characters with clear functional advantage. Increase in average mammalian brain size throughout the Tertiary provides a good example (Jerison 1973).

But we do not believe that most successful clades follow this route; they are more likely to be the progeny of parental species that managed to take advantage of rare opportunities occasionally provided when the earth's general equilibria are broken: unfilled ecospace around

newly-risen land, or a relatively empty world decimated by faunal catastrophe. The increasers may win simply by being first, not by being better in some Newtonian, mechanical sense; having been first, they may be able to hold on almost indefinitely, unless decimated themselves by a major diversity-independent episode of extinction. As R. Bakker (personal communication) argues, a principle of incumbency seems to hold for both the history of life and Western politics: it is very difficult for a better candidate to dislodge an entrenched occupant; an aspirant sits tight and awaits its opponent's demise—viz, Mesozoic mammals.

The virtual irrelevancy, in many cases, of morphological superiority to a clade's success may largely explain the puzzling observation that so few stories of increasing perfection in design can be read from the history of life. Our own initial surprise at this conclusion matches the insight that E. O. Wilson had (personal communication) when he set out to define biogeographical "success" in the con-

ventional terms of morphology and finally concluded that abundant, expanding, and widespread species are simply the *r*-selected, good colonists—not the "better" species in any usual sense of the term. The subset of increaser clades among survivors of diversity-independent mass extinction may be the "supertramps" of macroevolution (Diamond 1975).

History, as Hegel said, moves upward in a spiral of negations. We needed Simpson's "continuationism" between micro and macroevolution to rid paleontology of accumulated nonsense and to place it firmly among the evolutionary sciences. Secure in this status, paleontologists now need to emphasize that the higher-level study of long times and large clades requires a separate apparatus of evolutionary theory not fully available in the study of living organisms. We believe that the need to translate micro to macroevolution through the level of speciation guarantees that paleobiology shall not be a derivative field, but shall provide essential theory to any complete science of evolution.

V. Towards a General Philosophy of Change

Punctuated equilibria is a model for discontinuous tempos of change at one biological level only: the process of speciation and the deployment of species in geological time. Nonetheless, we believe that a general theory of punctuational change is broadly, though by no means exclusively, valid throughout biology.

The general preference that so many of us hold for gradualism is a metaphysical stance embedded in the modern history of Western cultures: it is not a high-order empirical observation, induced from the objective study of nature. The famous statement attributed to Linnaeus—*natura non facit saltum* (nature does not make leaps) may reflect some biological knowledge, but it also represents the translation into biology of the order, harmony and continuity that European rulers hoped to maintain in a society already assaulted by calls for fundamental social change (see A. O. Lovejoy's [1936] classic, *The Great Chain of Being*, for an extended discussion on gradualism as a metaphysic traced back to Aristotle and beyond).

When Darwin cleaved so strongly to grad-ualism—ignoring Huxley's advice that he did not need it to support the theory of natural selection—he translated Victorian society into biology where it need not reside. As his astute biographer W. Irvine remarks (1959, p. 98):

Darwin's matter was as English as his method. Terrestrial history turned out to be strangely like Victorian history writ large. . . . The economic conceptions [of laissez-faire liberalism] . . . can all be paralleled in the *Origin of Species*. But so, alas, can some of the doctrines of English political conservatism. In revealing the importance of time and the hereditary past, in emphasizing the persistence of vestigial structure, the minuteness of variations and the slowness of evolution, Darwin was adding Hooker and Burke [famous English conservatives] to Bentham and Adam Smith [equally famous liberals]. The constitution of the universe exhibited many of the virtues of the English constitution.

Karl Marx, who admired Darwin greatly and once stated that the *Origin* contained "the basis in natural history for all our views," made the same point in a famous letter to Engels (1862):

It is remarkable how Darwin recognizes among beasts and plants his English society with its division of labor, competition, opening up of new markets, 'invention,' and the Malthusian 'struggle for existence.' It is Hobbes' *'bellum omnium contra omnes,'* [war of all against all] and one is reminded of Hegel's *Phenomenology*, where civil society is described as a 'spiritual animal kingdom,' while in Darwin the animal kingdom figures as civil society.

We mention this not to discredit Darwin in any way, but merely to point out that even the greatest scientific achievements are rooted in their cultural contexts—and to argue that gradualism was part of the cultural context, not of nature.

Alternate conceptions of change have respectable pedigrees in philosophy. Hegel's dialectical laws, translated into a materialist context, have become the official "state philosophy" of many socialist nations. These laws of change are explicitly punctuational, as be-

fits a theory of revolutionary transformation in human society. One law, particularly emphasized by Engels, holds that a new quality emerges in a leap as the slow accumulation of quantitative changes, long resisted by a stable system, finally forces it rapidly from one state to another (law of the transformation of quantity into quality). Heat water slowly and it eventually transforms to steam; oppress the proletariat more and more, and guarantee the revolution. The official Soviet handbook of Marxism-Leninism (anonymous, undated) proclaims:

> The transition of a thing, through the accumulation of quantitative modifications, from one qualitative state to a different, new state, is a leap in development. . . . It is the transition to a new quality and signalizes a sharp turn, a radical change in development. . . . We often describe modern Darwinism as a theory of the evolution of the organic world, implying that this evolution covers both qualitative and quantitative changes. Leap-like qualitative changes in social life are designated by the concept of revolution. . . . The evolutionary development of society is inevitably consummated by leap-like qualitative transformation, by revolutions (anon., pp. 88–89).

It is easy to see the explicit ideology lurking behind this general statement about the nature of change. May we not also discern the implicit ideology in our Western preference for gradualism?

In the light of this official philosophy, it is not at all surprising that a punctuational view of speciation, much like our own, but devoid (so far as we can tell) of reference to synthetic evolutionary theory and the allopatric model, has long been favored by many Russian paleontologists (Ruzhentsev 1964; Ovcharenko 1969). It may also not be irrelevant to our personal preferences that one of us learned his Marxism, literally at his daddy's knee.

The punctuational view is also congenial with some important trends of Western thought during the twentieth century. Information theory, with its jargon of equilibrium, steady state, and homeostasis maintained by negative feedback—not to mention the extremely rapid transitions that occur with positive feedback—provides a goldmine of metaphor for advocates of punctuationism.

We emphatically do not assert the "truth" of this alternate metaphysic of punctuational change. Any attempt to support the exclusive validity of such a monistic, a priori, grandiose notion would verge on the nonsensical. We believe that gradual change characterizes some hierarchical levels, even though we may attribute it to punctuation at a lower level—the macroevolutionary trend produced by species selection, for example. We make a simple plea for pluralism in guiding philosophies—and for the basic recognition that such philosophies, however hidden and inarticulated, do constrain all our thought.

Nonetheless, we do believe that the punctuational metaphysic may prove to map tempos of change in our world better and more often than any of its competitors—if only because systems in steady state are not only common but also so highly resistant to change. We believe that the punctuational view will become important in evolutionary biology at levels both lower and higher than the events of speciation covered in our model of punctuated equilibria. Dodson (1975, 1976) has made a promising start, partly in explicit analogy with our model, towards the application of Thom's "catastrophe theory" (a punctuational topology) to change within populations. At the next level of speciation, Carson (1975) has proposed a model that is punctuational even in ecological time. He argues that sexual, diploid organisms possess two differing systems of genetic variability: 1) An "open" system of freely-recombining, polymorphic loci responsible for gradual, adaptive change within populations—e.g. clinal and subspecific variability. 2) A "closed" system of co-adapted, internally balanced gene complexes that cannot vary without drastic effects on the ontogenetic program of a species; thus, the "closed" system varies between, but not within, species. Gradualistic models work only for the adaptations that arise within populations by a fine-tuning of organism to environment; for these adaptations reflect change in the open system. But these gradual changes cannot be extrapolated to a model for speciation, because the origin of new taxa involves rapid, drastic reorganization of the closed system. Speciation, the source of macroevolutionary variation, is qualitatively dif-

ferent from local adaptation within populations. It is also punctuational in ecological time. Carson writes (1975, pp. 87–88):

> The classical view of speciation holds that it is a gradual microevolutionary process. Thus, the genetic events which lead toward speciation are considered to be individually trivial or simple. Changes, such as a shift in gene frequency, may accumulate slowly in a population. This view does not invoke any unusual or quantum set of changes for the origin of interspecific differences. . . . Most theories of speciation are thus wedded to gradualism, using the mode of origin of intraspecific adaptations as a model. . . . I would nevertheless like to propose that the following possibility be seriously considered. Speciational events may be set in motion and important genetic saltations towards species formation accomplished by a series of catastrophic, stochastic genetic events. . . . Speciation is considered to be initiated when an unusual forced reorganization of the epistatic supergenes of the closed variability system occurs. . . . I propose that this cycle of disorganization and reorganization be viewed as the essence of the speciation process. Under most circumstances, it seems unlikely that gradual microevolutionary changes could easily accomplish the drastic changes in the closed system which seem to be required.

Carson argues that these reorganizations of the closed system may occur very rapidly when natural selection is relaxed during a population flush-crash-founder cycle.

At the higher level of evolutionary transition between basic morphological designs, gradualism has always been in trouble, though it remains the "official" position of most Western evolutionists. Smooth intermediates between *Baupläne* are almost impossible to construct, even in thought experiments; there is certainly no evidence for them in the fossil record (curious mosaics like *Archaeopteryx* do not count). Even so convinced a gradualist as G. G. Simpson (1944) invoked quantum evolution and inadaptive phases to explain these transitions. Recently, Lovtrup (1974) and Frazzetta (1975) have written books to support a punctuational theory for the origin

of new *Baupläne*. We believe that a coherent, punctuational theory, fully consistent with Darwinism (though not with Darwin's own unnecessary preference for gradualism), will be forged from a study of the genetics of regulation, supported by the resurrection of long-neglected data on the relationship between ontogeny and phylogeny (see Gould 1977). Ager (1973, p. 100), whose small book advocates a punctuational view of the stratigraphic record, speaks in simile of the tempo that we support as most characteristic of the way our world works: "The history of any one part of the earth, like the life of a soldier, consists of long periods of boredom and short periods of terror."

VI. Suggestions for a Program of Research

Cosmic philosophical waffling aside, our highest hope for punctuated equilibria is that it might guide a change in paleobiological practice. We believe that the agenda of paleobiology should accord a prominent place to establishing the unbiased empirical distribution of evolutionary tempos; our model makes this possible by tabulating as data several important phenomena previously ignored. We suggest the following as a protocol for the further testing and utility of punctuated equilibria:

1. In testing for gradualism vs. punctuation in individual taxa, study the geographic variability of species over their entire preserved range. Do not confine a study to local sections or single cores.

2. Study the distribution of evolutionary tempos for *all* members of an ecosystem or community. We hope that the emphasis in testing our model will shift away from abstracted individual cases towards the unbiased assessment of entire faunas; for, as we have emphasized throughout this paper, the essential question is one of *relative frequency*. We hope that all students engaged in such work will keep our favorite motto before them: stasis is data. As MacGillavry wrote (1968, p. 70): "What, to my knowledge, is completely lacking, is a quantitative study of the entire fauna of such successions. A study of this kind should pay attention to the percentage of forms which do not show any evolutionary change."

Of our two most important predictions for local sections—"sudden" transition from ancestor to descendant and stasis within individual taxa—we regard stasis as more amenable to study. Morphological breaks can usually be attributed equally well to punctuated equilibria or to an imperfect record. But stasis in a great majority of taxa—particularly for the characters used to define species—speaks clearly for us, while a high frequency of directional change would speak just as strongly against us. Moreover, the relative frequency for stasis can be tabulated with value even in local sections, for gradualism predicts that in situ change will be directional.

3. With a model that allows us to assess relative frequency, a basic evolutionary question about phyletic gradualism can finally be posed—where and how often? In what ecological situations does it occur? Is it unusually common in certain taxa? We have already suggested that the frequency of gradualism might be higher in asexual species because their "continuous" trends are produced by clone selection, punctuational at a lower level. These data are important for evolutionary theory, and they could not be gathered when paleontologists regarded cases of gradualism as the only legitimate illustrations of evolution.

4. Study general patterns in the history of diversity, whenever possible, at the species level. The species, in our view, is a true, basic and stable evolutionary unit, not merely an intermediate rank in a hierarchy from individual to kingdom, defined as an arbitrary segment of a continuously changing lineage. It is ironic that so much paleontological activity has been devoted to the description of species, but that virtually all interpretive studies concentrate on generic and higher rank. The reason for this has been expediency, not desire. Many evolutionists have lamented the spottiness and inconsistency of species-level taxonomy in the fossil record, and have studied genera and families *faute de mieux*. We agree that students of macroevolution cannot merely tabulate species from the primary literature. But Stanley (1975a, 1976) has devised some ingenious methods for reliable inferences about the origination, duration, and extinction of species in larger clades.

5. Test Wright's Rule as a precondition for species selection. Are the morphological di-

rections of speciation within a clade random with respect to the direction of evolutionary trends? They need not be: it is quite possible, for example, that most species will arise at sizes larger than their ancestors within a clade exhibiting Cope's Rule as a general trend. In such a case, species selection would play no creative role, just as natural selection would not direct evolution within populations if mutations occurred preferentially in adaptive directions. (Natural selection might still eliminate the unfit, but the central postulate of Darwinian theory—that natural selection creates the fit—would collapse.) If Wright's Rule fails in favor of a preferential tendency for speciation toward the general direction of a larger trend, then species selection is not needed because a random removal of species would still yield the trend.

Wright's Rule also requires that speciation be common in order to provide enough raw material for species selection. We therefore predict that the left end of Van Valen's (1973) random extinction curves will actually be concave rather than straight as he depicts them—leading to a marked increase of species with very short durations. (These are the easiest species to miss in the fossil record, and the straightness of a raw, empirical line for a sample biased by geological constraints might imply concavity in the true universe. This could be tested by asking whether groups with better records yield greater concavity.) Large numbers of species with short durations would supply a sufficient pool of variability for species selection.

In bringing paleontology within the modern synthesis, Simpson emphasized evolutionary rates and strongly advocated their further study. Yet rather little has come of his plea, primarily, we believe, because underlying assumptions of gradualism yielded much in the way of discouragement and rather little in concrete suggestions for research. Since the 1940's, paleontology has undertaken several long excursions in other directions—particularly into the functional morphology of individual taxa and the reconstruction of fossil communities. These studies, at their best, have been elegant and persuasive; they have certainly been of great value. But they have not produced new evolutionary theory; they have not asserted the theoretical independence of paleobiology; they have, in essence, shown

that fossil organisms and assemblages work much as modern ones; they have, in this sense, continued the tradition of paleobiology as a derivative science, indebted for all its insights to the evolutionary biology of modern organisms and ready to provide nothing but simple confirmation in return. But why be a paleontologist if we are condemned only to verify imperfectly what students of living organisms can propose directly? An evolutionary theorist should pursue paleobiology only if he believes that the direct study of geological time can yield new insights to enlarge a theory constructed for events in ecological time. We believe that paleobiology can do this. Let us now heed Simpson's recommendation of thirty years past. The study of evolutionary tempos lies in the exclusive domain of paleobiology. It is, we believe, our most promising arena for the derivation of independent macroevolutionary theories. Conceptual tools are now available for a fruitful study of evolutionary tempos and modes.

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