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PUNCTUATED EQUILIBRIA: AN ALTERNATIVE TO PHYLETIC GRADUALISM

Niles Eldredge · *Stephen Jay Gould*

Editorial introduction. Moving from populations to species, we recall that the process of speciation as seen through the hyperopic eyes of the paleontologist is an old and venerable theme. But the significance of "gaps" in the fossil record has been a recurrent "difficulty," used on the one hand to show that spontaneous generation is a "fact," and on the other hand to illustrate the "incompleteness" of the fossil record. Some have expressed a third interpretation, which views such gaps as the logical and expected result of the allopatric model of speciation.

Bernard's Eléments de Paléontologie (1895) discusses the existence of gaps in the fossil record as follows, p. 25, English edition:

> Still it remains an indisputable fact that in the most thoroughly explored regions, those where the fauna is best known, as, for instance, the Tertiary of the Paris basin, the species of one bed often differ widely from those of the preceding, even where no stratigraphic gap appears between them. This is easily explained. The production of new forms usually takes place within narrowly limited regions. It may happen in reality that one form evolves in the same manner in localities widely separated from each other, and farther on we shall see examples of this: but this is not generally the case, the area of the appearance of species is

usually very circumscribed. This fact has been established in the case of certain butterflies and plants. The diversity having once occurred, the new types spread often to great distances, and may be found near the present form without crossing with it or presenting any trace of transition.

The same phenomenon must have taken place in former epochs. It is then only by the merest chance that geologists are able to locate the origin of the species they have under consideration; if, furthermore, the phenomena of erosion or metamorphism have destroyed or changed the locality in question, direct observation will not furnish any means of supplying the missing links of the chain.

Although this has been pointed out nicely by Bernard—and moreover, any number of paleontologists will tell you that this is what they teach—comprehension and application are two different things. And indeed, the fossil record has been interpreted by many to show just the opposite. J. B. S. Haldane's classical *The Cause of Evolution*, published in 1932, contains the following passage (p. 213):

> But [Sewall] Wright's theory [that evolution is most rapid in populations large enough to be reasonably variable, but small enough to permit large changes in gene frequencies due to random drift] certainly supports the view taken in this book that the evolution in large random-mating populations, which is recorded by paleontology, is not representative of evolution in general, and perhaps gives a false impression of the events occurring in less numerous species.

Thus an extremely eminent student of the evolutionary process considered that the known fossil record supported the view of evolution proceeding as a stately unfolding of changes in large populations.

The interpretation supported by Eldredge and Gould is that allopatric speciation in small, peripheral populations *automatically* results in "gaps" in the fossil record. Throughout their essay, however, runs a larger and more important lesson: *a priori* theorems often determine the results of "empirical" studies, before the first shred of evidence is collected. This idea, that theory dictates what one sees, cannot be stated too strongly.

Statement

In this paper we shall argue:

(1) The expectations of theory color perception to such a degree that new notions seldom arise from facts collected under the influence of old pictures of the world. New pictures must cast their influence before facts can be seen in different perspective.

(2) Paleontology's view of speciation has been dominated by the picture of "phyletic gradualism." It holds that new species arise from the slow and steady transformation of entire populations. Under its influence, we seek unbroken fossil series linking two forms by insensible gradation as the only complete mirror of Darwinian processes; we ascribe all breaks to imperfections in the record.

(3) The theory of allopatric (or geographic) speciation suggests a different interpretation of paleontological data. If new species arise very rapidly in small, peripherally isolated local populations, then the great expectation of insensibly graded fossil sequences is a chimera. A new species does not evolve in the area of its ancestors; it does not arise from the slow transformation of all its forbears. Many breaks in the fossil record are real.

(4) The history of life is more adequately represented by a picture of "punctuated equilibria" than by the notion of phyletic gradualism. The history of evolution is not one of stately unfolding, but a story of homeostatic equilibria, disturbed only "rarely" (i.e., rather often in the fullness of time) by rapid and episodic events of speciation.

The Cloven Hoofprint of Theory

> Innocent, unbiased observation is a myth.
>
> P. B. Medawar (1969, p. 28)

Isaac Newton possessed no special flair for the turning of phrases. Yet two of his epigrams have been widely cited as guides for the humble and proper scientist—his remark in a letter of 1675 written to Hooke: "If I have seen farther, it is by standing on the shoulders of giants," and his confusing comment of the *Principia* (1726 edition, p. 530): "hypotheses non fingo"—[I frame no hypotheses]. The first is not his own; it has a pedigree extending back at least to Bernard of Chartres in 1126 (Merton, 1965). The second is his indeed, but modern philosophers have offered as many interpretations for it as the higher critics heaped upon Genesis 1 in their heyday (see Mandelbaum, 1964, p. 72 for a bibliography).

Although most scholars would now hold, with Hanson (1969, 1970, see also Koyré, 1968), that Newton meant only to eschew idle speculation and untestable opinion, his phrase has traditionally been interpreted in another light—as the credo of an inductivist philosophy that views "objective" fact as the primary input to science and theory as the generalization of this unsullied information. For example, Ernst Mach, the great physicist-philosopher, wrote (1893, p. 193): "Newton's reiterated and emphatic protestations that he is not concerned with hypotheses as to the causes of phenomena, but has simply to do with the investigation and transformed statement of *actual facts* . . . stamps him as a philosopher of the *highest* rank."

Today, most philosophers and psychologists would brand the inductivist credo as naive and untenable on two counts:

(1) We do not encounter facts as *data* (literally "given") discovered objectively. All observation is colored by theory and expectation. (See Vernon, 1966, on the relation between expectation and perception. For a radical view, read Feyerabend's (1970) claim that theories act as "party lines" to force observation in preset channels, unrecognized by adherents who think they perceive an objective truth.)

(2) Theory does not develop as a simple and logical extension of observation; it does not arise merely from the patient accumulation of facts. Rather, we observe in order to test hypotheses and examine their consequences. Thus, Hanson (1970, pp. 22–23) writes: "Much recent philosophy of science has been dedicated to disclosing that a 'given' or a 'pure' observation language is a myth-eaten fabric of philosophical fiction. . . . In any observation statement the cloven hoofprint of theory can readily be detected."

Yet, inductivist notions continue to control the methodology and ethic of practicing scientists raised in the tradition of British empiricism. In unguarded moments, great naturalists have correctly attributed their success to skill in hypothesizing and power in imagination; yet, in the delusion of conscious reflection, they have usually ascribed their accomplishments to patient induction. Thus, Darwin, in a statement that should be a motto for all of us (letter to Fawcett, September 18, 1861, quoted in Medawar, 1969), wrote:

> About thirty years ago there was much talk that geologists ought only to observe and not theorize; and I well remember someone saying that at this rate a man might as well go into a gravel-pit and count the pebbles and describe the colours. How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service.

Yet, in traditional obeisance to inductivist tenets, he wrote in his autobiography that he had "worked on true Baconian principles, and without any theory collected facts on a wholesale scale" (see discussion of this point in Ghiselin, 1969a; Medawar, 1969; and de Beer, 1970).

Almost all of us adhere, consciously or unconsciously, to the inductivist methodology. We do not recognize that all our perceptions and descriptions are made in the light of theory. Leopold (1969, p. 12), for example, claimed that he could describe and analyze the aesthetics of rivers "without introduction of any personal preference or bias." He began by generating "uniqueness" values, but abandoned that approach when the sluggish, polluted, murky Little Salmon River scored highest among his samples. He then selected a very small subset of his measures for a simplified type of multivariate scaling. As he must have known before he started, Hells Canyon of the Snake River now ranked best. It cannot be accidental that the article was

written by an opponent to applications then before the Federal Power Commission for the damming of Hells Canyon. (It is no less fortuitous that so many philosophers, Hegel and Spencer in particular, generated ideal states by pure reason that mirrored their own so well.)

In paleontology, even the most "objective" undertaking, the "pure" description of fossils, is all the more affected by theory because that theory is unacknowledged. We describe part by part and are led, subtly but surely, to the view that complexity is irreducible. Such description stands against a developing science of form (Gould, 1970a, 1971a) because it both gathers different facts (static states rather than dynamic correlations) and presents contrary comparisons (compendia of differences rather than reductions of complexity to fewer generating factors). D'Arcy Thompson, with his usual insight, wrote of the "pure" taxonomist (1942, p. 1036), "when comparing one organism with another, he describes the differences between them point by point and 'character' by 'character.' If he is from time to time constrained to admit the existence of 'correlation' between characters . . . yet all the while he recognizes this fact of correlation somewhat vaguely, as a phenomenon due to causes which, except in rare instances, he can hardly hope to trace; and he falls readily into the habit of thinking and talking of evolution as though it had proceeded on the lines of his own description, point by point and character by character."

The inductivist view forces us into a vicious circle. A theory often compels us to see the world in its light and support. Yet, we think we see objectively and therefore interpret each new datum as an independent confirmation of our theory. Although our theory may be wrong, we cannot confute it. To extract ourselves from this dilemma, we must bring in a more adequate theory; it will not arise from facts collected in the old way. Paleontology supported creationism in continuing comfort, yet the imposition of Darwinism forced a new, and surely more adequate, interpretation upon old facts. Science progresses more by the introduction of new world-views or "pictures"* than by the steady accumulation of information.

This issue is central to the study of speciation in paleontology. We believe that an inadequate picture has been guiding our thoughts on speciation for 100 years. We hold that its influence has been all the more tenacious because paleontologists, in claiming that they see objectively, have not recognized its guiding sway. We contend that a notion developed elsewhere, the theory of allopatric speciation, supplies a more satisfactory picture for the ordering of paleontological data.

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* We have no desire to enter the tedious debate over what is, or is not, a "model," "theory," or "paradigm" (Kuhnian, not Rudwickian). In using the neutral word "picture," we trust that readers will understand our concern with alternate ways of seeing the world that render the same facts in *different* ways.

Phyletic Gradualism: Our Old and Present Picture

Je mehr sich das palaeontologische Material vergrössert, desto zahlreicher und vollständiger werden die Formenreihen.

Zittel, 1895, p. 11

Charles Darwin viewed the fossil record more as an embarrassment than as an aid to his theory. Why, he asked (1859, p. 310), do we not find the "infinitely numerous transitional links" that would illustrate the slow and steady operation of natural selection? "Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graduated organic chain; and this, perhaps, is the gravest objection which can be urged against my theory" (1859, p. 280). Darwin resolved this dilemma by invoking the great inadequacy of surviving evidence (1859, p. 342): "The geological record is extremely imperfect and this fact will to a large extent explain why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduated steps. He who rejects these views on the nature of the geological record, will rightly reject my whole theory."

Thus, Darwin set a task for the new science of evolutionary paleontology: to demonstrate evolution, search the fossil record and extract the rare exemplars of Darwinian processes—insensibly graded fossil series, spared somehow from the ravages of decomposition, non-deposition, metamorphism, and tectonism. Neither the simple testimony of change nor the more hopeful discovery of "progress" would do, for anti-evolutionists of the catastrophist schools had claimed these phenomena as consequences of their own theories. The rebuttal of these doctrines and the test for (Darwinian) evolution could only be an *insensibly graded fossil sequence*—this discovery of all transitional forms linking an ancestor with its presumed descendant (*figure 5–1*). The task that Darwin set has guided our studies of evolution to this day.*

In titling his book *On the Origin of Species by Means of Natural Selection*, Darwin both identified this event as the keystone of evolution and stated his belief in its manner of occurrence. New species can arise in only two ways: by the transformation of an entire population from one state to another (phyletic evolution) or by the splitting of a lineage (speciation). The second process must occur: otherwise there could be no increase in numbers of taxa and life would cease as lineages became extinct. Yet, as Mayr (1959) noted, Darwin muddled this distinction and cast most of his discussion in terms of phyletic

* Beliefs in "saltative" evolution, buttressed by de Vries' "mutation theory," collapsed when population geneticists of the 1930's welded modern genetics and Darwinism into our "synthetic theory" of evolution. The synthetic theory is completely Darwinian in its identification of natural selection as the efficient cause of evolution.

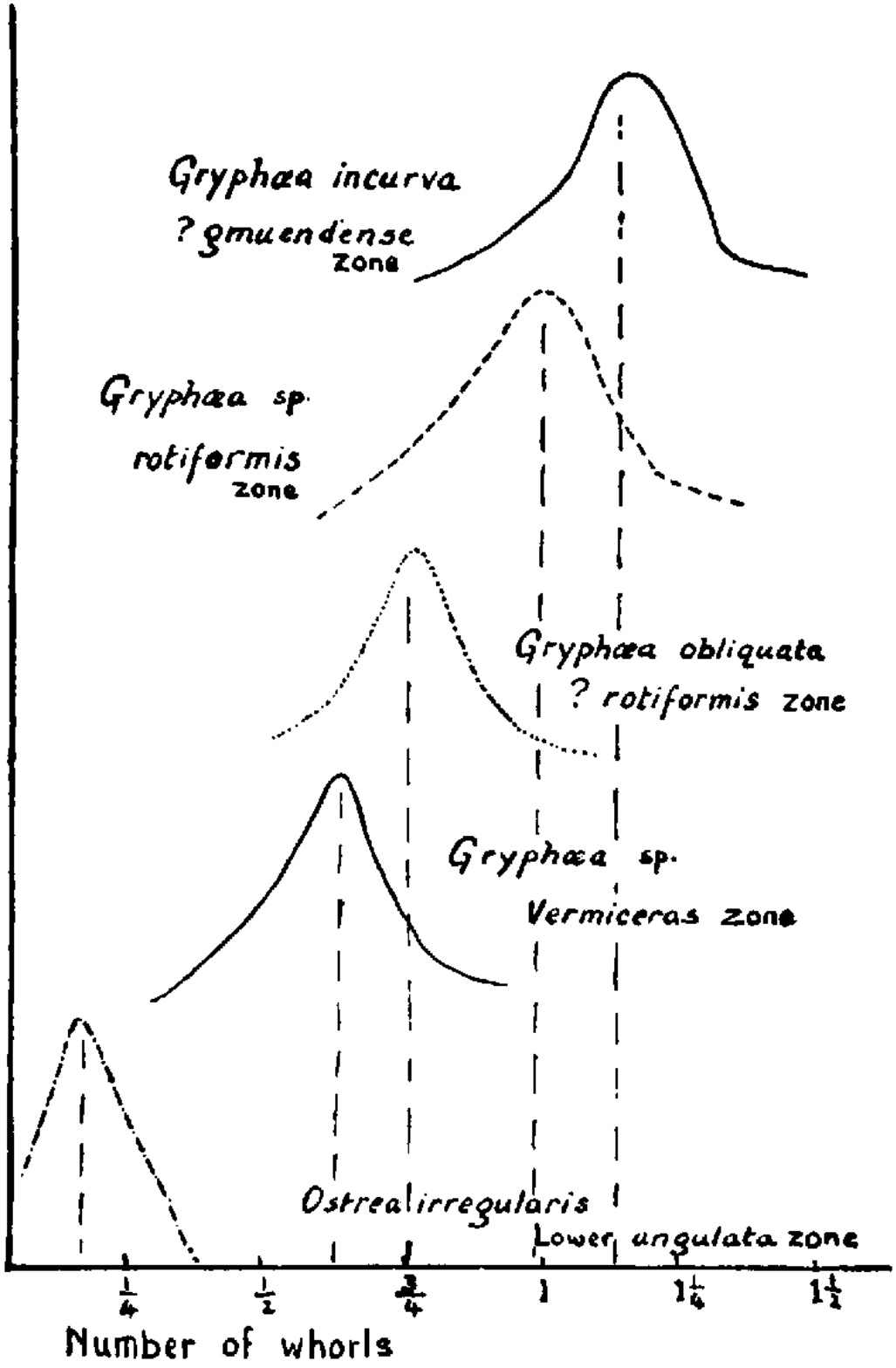

Figure 5–1: The classic case of postulated phyletic gradualism in paleontology. Slow, progressive, and gradual increase in whorl number in the basal Liassic oyster *Gryphaea*. From Trueman, 1922; figure 5.

evolution. His insistence on insensibly graded sequences among fossils reflects this emphasis, for if species arise by the gradual transformation of entire populations, an even sequence of intermediates should indeed be found. When Darwin did discuss speciation (the splitting of lineages), he

continued to look through the glasses of transformation: he saw splitting largely as a sympatric process, proceeding slowly and gradually, and producing progressive divergence between forms. To Darwin, therefore, speciation entailed the same expectation as phyletic evolution: a long and insensibly graded chain of intermediate forms. Our present texts have not abandoned this view (*figure 5–2*), although modern biology has.

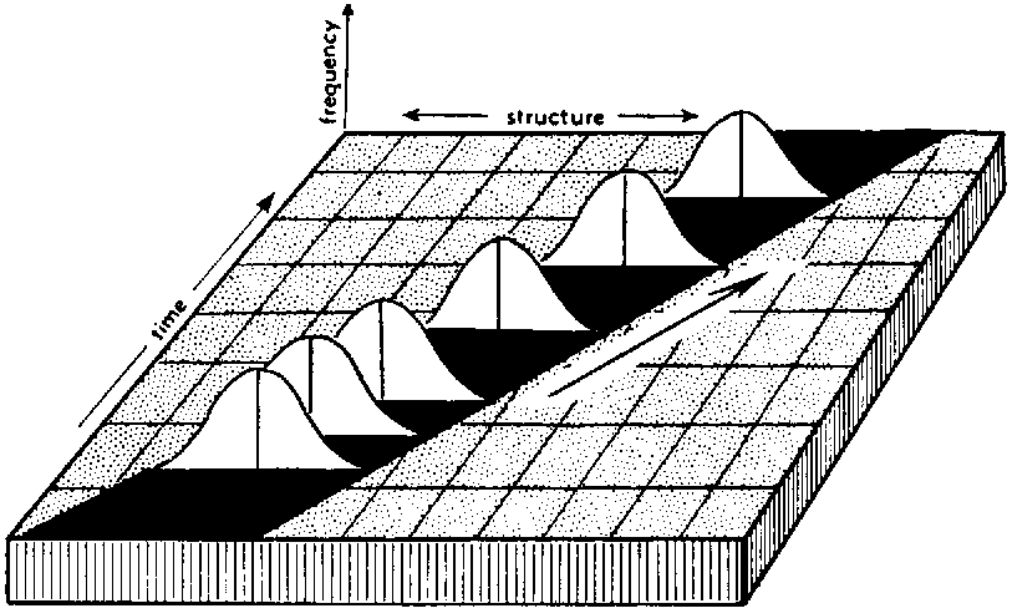

Figure 5–2: A standard textbook view of evolution *via* phyletic gradualism. From Moore, Lalicker, and Fischer, 1952; figure 1–14.

In this Darwinian perspective, paleontology formulated its picture for the origin of new taxa. This picture, though rarely articulated, is familiar to all of us. We refer to it here as "phyletic gradualism" and identify the following as its tenets:

(1) New species arise by the transformation of an ancestral population into its modified descendants.

(2) The transformation is even and slow.

(3) The transformation involves large numbers, usually the entire ancestral population.

(4) The transformation occurs over all or a large part of the ancestral species' geographic range.

These statements imply several consequences, two of which seem especially important to paleontologists:

(1) Ideally, the fossil record for the origin of a new species should consist of a long sequence of continuous, insensibly graded intermediate forms linking ancestor and descendant.

(2) Morphological breaks in a postulated phyletic sequence are due to imperfections in the geological record.

Under the influence of phyletic gradualism, the rarity of transitional series remains as our persistent bugbear. From the reputable claims of a Cuvier or an Agassiz to the jibes of modern cranks and fundamentalists, it has stood as the bulwark of anti-evolutionist arguments: "For evolution to be true, there had to be thousands, millions of transitional forms making an unbroken chain" (Anon., 1967—from a Jehovah's Witnesses pamphlet).

We have all heard the traditional response so often that it has become imprinted as a catechism that brooks no analysis: the fossil record is extremely imperfect. To cite but one example: "The connection of arbitrarily selected 'species' in a time sequence, in fact their complete continuity with one another, is to be expected in all evolutionary lineages. But, *fortunately*, because of the imperfect preservation of fossil faunas and floras, we shall meet relatively few examples of this, no matter how long paleontology continues" (Eaton, 1970, p. 23—our italics; we are amused by the absurdity of a claim that we should rejoice in a lack of data because of the taxonomic convenience thus provided).

This traditional approach to morphological breaks merely underscores what Feyerabend meant (see above) in comparing theories to party lines, for it renders the picture of phyletic gradualism virtually unfalsifiable. The picture prescribes an interpretation and the interpretation, viewed improperly as an "objective" rendering of data, buttresses the picture. We have encountered no dearth of examples, and cite the following nearly at random. Neef (1970) encountered "apparent saltation in the *Pelicaria* lineage" (p. 464), a group of Plio-Pleistocene snails. Although he cites no lithologic or geographic data favoring either interpretation, the picture of phyletic gradualism prescribes a preference: "It is likely that the discontinuity . . . is due to a period of non-deposition. . . . The possibility that the apparent saltations in the *Pelicaria* lineage are due to the migration of advanced forms from small nearby semi-isolated populations and that deposition of the Marima Sandstone was continuous cannot be entirely excluded" (1970, p. 454).

Moreover, the picture's influence has many subtle extensions. For instance:

(1) It colors our language. We are compelled to talk of "morphological breaks" in order to be understood. But the term is not a neutral descriptor; it presupposes the truth of phyletic gradualism, for a "break" is an interruption of something continuous. (Under a deVriesian picture, for example, "breaks" are "saltations"; they are real and expressive of evolutionary processes.)

(2) It prescribes the cases that are worthy of study. If breaks are artificial, the sequences in which they abound become, *ipso facto*, poor objects for evolutionary investigation. But surely there is something insidious here: if breaks are real and stand against the picture of phyletic gradualism, then the picture itself excludes an investigation of the very cases that could place it in jeopardy.

If we doubt phyletic gradualism, we should not seek to "disprove" it "in the rocks." We should bring a new picture from elsewhere and see if it provides a more adequate interpretation of fossil evidence. In the next section, we express our doubts, display a different picture, and attempt this interpretation.

But before leaving the picture of phyletic gradualism, we wish to illustrate its pervasive influence in yet another way. Kuhn (1962) has stressed the impact of textbooks in molding the thought of new professionals. The "normal science" that they inculcate is "a strenuous and devoted attempt to force nature into the conceptual boxes supplied by professional education" (1962, p. 5).

Before the "modern synthesis" of the 1930's and 40's, English-speaking invertebrate paleontologists were raised upon two texts—Eastman's translation of Zittel (1900) and that venerable *Gray's Anatomy* of British works, Woods' *Palaeontology* (editions from 1893 to 1946, last edition reprinted five times before 1958 and still very much in use). Both present an orthodox version of phyletic gradualism. In a classic statement, ending with the sentence that serves as masthead to this section, Zittel wrote (Eastman translation, 1900, p. 10):

> Weighty evidence for the progressive evolution of organisms is afforded by fossil transitional series, of which a considerable number are known to us, notwithstanding the imperfection of the palaeontological record. By transitional series are meant a greater or lesser number of similar forms occurring through several successive horizons, and constituting a practically unbroken morphic chain . . . With increasing abundance of palaeontological material, the more numerous and more complete are the series of intermediate forms which are brought to light.

The last edition of Woods (1946) devotes three pages to evolution; all but two paragraphs (one on ontogeny, the other on orthogenesis) to an exposition of phyletic gradualism (one page on the imperfection of the record, another on some rare examples of graded sequences).

Our current textbooks have changed the argument not at all. Moore, Lalicker and Fischer (1952, p. 30), in listing the fossil record among "evidences of evolution," have only this to say about it: "Although lack of knowledge is immeasurably greater than knowledge, many lineages among fossils of various groups have been firmly established. These demonstrate the transformation of one species or genus into another and thus constitute documentary evidence of gradual evolution." And Easton (1960, p. 34), citing the apotheosis of our achievements, writes: "An evolutionary series represents the peak of scientific accomplishment in organizing fossil invertebrates. It purports to show an orderly progression in morphologic changes among related creatures during successive intervals of time."

That these older texts hold so strongly to phyletic gradualism should surprise no one; harder to understand is the fact that virtually all modern texts repeat the same arguments even though their warrant had disappeared, as we shall now show, with the advent of the allopatric theory of speciation.

The Biospecies and Punctuated Equilibria: A Different Picture of Speciation

> Habits of thought in the tradition of a science are not readily changed, it is not easy to deviate from the customary channels of accumulated experience in conventionalized subjects.
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> G. L. Jepsen, 1949, p. v

An irony. The formulation of the biological species concept was a major triumph of the synthetic theory (Mayr, 1963, abridged and revised 1970, remains the indispensable source on its meaning and implications). Since paleontology has always taken its conceptual lead from biology (with practical guidance from geology), it was inevitable that paleontologists should try to discover the meaning of the biospecies for their own science.

Here we meet an ironic situation: the taxonomic perspective—one of our persistent albatrosses—dictated an approach to the biospecies. Instead of extracting its insights about evolutionary processes, we sought only its prescriptions for classification. We learned that species are populations, that they are recognized in fossils by ranges of variability not by correspondence to idealized types. The "new systematics" ushered in the revolution in species-level classification that Darwin's theory had implied but not effected. In paleontology, its main accomplishment has been a vast condensation and elimination of spurious taxa established on typological criteria.

But the new systematics also rekindled a theoretical debate unsurpassed in the annals of paleontology for its ponderous emptiness: What is the nature of a paleontological species? In this reincarnation: can taxa designated as biospecies be recognized from fossils? Biologists insisted that the biospecies is a "real" unit of nature, a population of interacting individuals, reproductively isolated from all other groups. Yet its reality seemed to hinge upon what Mayr calls its "non-dimensional" aspect: species are distinct at any moment in time, but the boundaries between forms must blur in temporal extension—a continuous lineage cannot be broken into objective segments. Attempts to reconcile or divorce the non-dimensional biospecies and the temporal "paleospecies" creep on apace (Imbrie, 1957; Weller, 1961; McAlester, 1962; Shaw, 1969; and an entire symposium edited by Sylvester-Bradley, 1956); if obfuscation is any sign of futility, we offer the following as a plea for the termination of this discussion: "Such a plexiform lineage . . .

constitutes a chronospecies (or paleospecies), and it is composed of many successional polytypic morphospecies ('holomorphospecies'), each of which is in theory the paleontological equivalent of a neontological biospecies" (Thomas, 1956, p. 24).

The discussion is futile for a very simple reason: the issue is insoluble; it is not a question of fact (phylogeny proceeds as it does no matter how we name its steps), but a debate about ways of ordering information. When Whitehead said that all philosophy was a footnote to Plato, he meant not only that Plato had identified all the major problems, but also that the problems were still debated because they could not be solved. The point is this: the hierarchical system of Linnaeus was established for his world: a world of discrete entities. It works for the living biota because most species are discrete at any moment in time. It has no objective application to evolving continua, only an arbitrary one based on subjective criteria for division. Linnaeus would not have set up the same system for our world. As Vladimir Nabokov writes in *Ada* (1969, p. 406): "Man . . . will never die, because there may never be a taxonomical point in his evolutionary progress that could be determined as the last stage of man in the cline turning him into Neohomo, or some horrible throbbing slime."

Then does the biospecies offer us nothing but semantic trouble? On one level, the answer is no because it can be applied with great effectiveness to past time-planes. But on another level, and this involves our irony, we must avoid the narrow approach that embraces a biological concept only when it can be transplanted bodily into our temporal taxonomy. The biospecies abounds with implications for the operation of evolutionary processes. Instead of attempting vainly to name successional taxa objectively in its light (McAlester, 1962), we should be applying its concepts. In the following section, we argue that one of these concepts—the theory of allopatric speciation—might reorient our picture for the origin of taxa.

Implications of allopatric speciation for the fossil record. We wish to consider an alternate picture to phyletic gradualism; it is based on a theory of speciation that arises from the behavior, ecology, and distribution of modern biospecies. First, we must emphasize that mechanisms of speciation can be studied directly only with experimental and field techniques applied to living organisms. No theory of evolutionary mechanisms can be generated directly from paleontological data. Instead, theories developed by students of the modern biota generate predictions about the course of evolution in time. With these predictions, the paleontologist can approach the fossil record and ask the following question: Are observed patterns of geographic and stratigraphic distribution, and apparent rates and directions of morphological change, consistent with the consequences of a particular theory of speciation? 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.*

During the past thirty years, the allopatric theory has grown in popularity to become, for the vast majority of biologists, *the* theory of speciation. Its only serious challenger is the sympatric theory. Here we discuss only the implications of the allopatric theory for interpreting the fossil record of sexually-reproducing metazoans. We do this simply because it is the allopatric, rather than the sympatric, theory that is preferred by biologists. We shall therefore contrast the allopatric theory with the picture of phyletic gradualism developed in the last section.

Most paleontologists, of course, are aware of this theory, but the influence of phyletic gradualism remains so strong that discussions of geographic speciation are almost always cast in its light: geographic speciation is seen as the slow and steady transformation of two separated lineages—i.e., as *two* cases of phyletic gradualism (*figure 5–3*). Raup and Stanley (1971, p. 98), for example, write:

> Let us consider populations of a species living at a given time but not in geographic contact with each other. . . . Two or more segments of the species thus evolve and undergo *phyletic* speciation independently. . . . The distinction between phyletic and geographic speciation is to some extent artificial in that both processes depend on natural selection. The critical difference is that phyletic speciation is accomplished in the absence of geographic isolation and geographic speciation requires geographic isolation (italics ours).

The central concept of allopatric speciation is that new species can arise only when a small local population becomes isolated at the margin of the geographic range of its parent species. Such local populations are termed *peripheral isolates*. A peripheral isolate develops into a new species if *isolating mechanisms* evolve that will prevent the re-initiation of gene flow if the new form re-encounters its ancestors at some future time. As a consequence of the allopatric theory, new fossil species do not originate in the place where their ancestors lived. It is extremely improbable that we shall be able to trace the gradual splitting of a lineage merely by following a certain species up through a local rock column.

Another consequence of the theory of allopatric processes follows: since selection always maintains an equilibrium between populations and their local environment, the morphological features that distinguish the descendant

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* The rate and direction of morphological change over long periods of time is the most obvious kind of evolutionary pattern that we can test against predictions based on processes observed over short periods of time by neontologists. We try to do this in the next section.

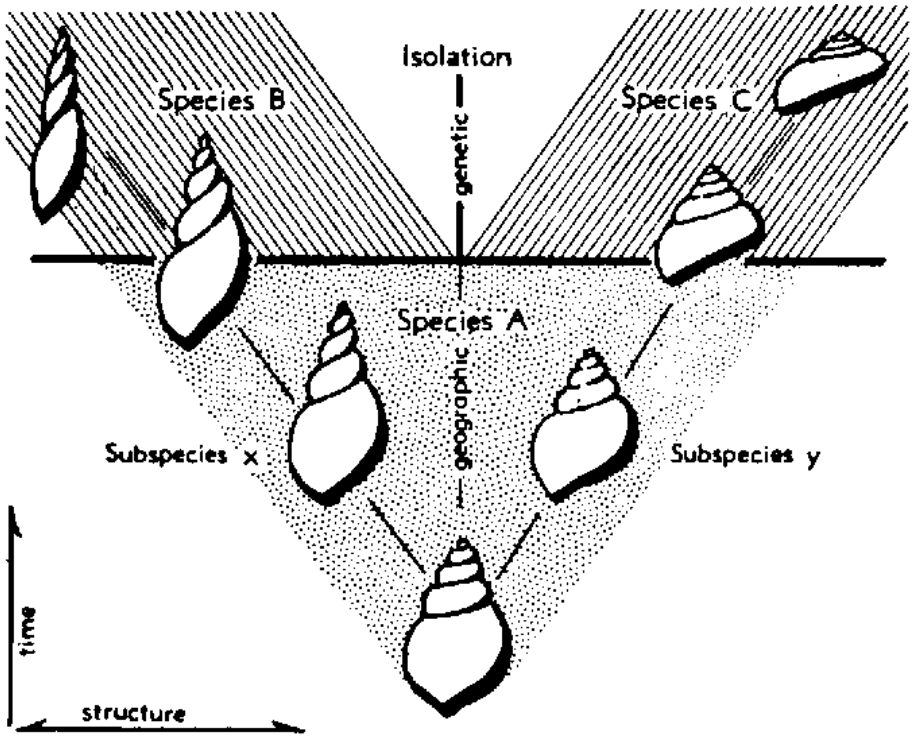

Figure 5–3: A hypothetical case of geographic speciation viewed from the perspective of phyletic gradualism—slow and gradual transformation in two lineages. From Moore, Lalicker, and Fischer, 1952; figure 1–15.

species from its ancestor are present close after, if not actually prior to, the onset of genetic isolation. These differences are often accentuated if the two species become sympatric at a later date (character displacement—Brown and Wilson, 1956). In any event, most morphological divergence of a descendant species occurs very early in its differentiation, when the population is small and still adjusting more precisely to local conditions. After it is fully established, a descendant species is as unlikely to show gradual, progressive change as is the parental species. Thus, in the fossil record, we should not expect to find gradual divergence between two species in an ancestral-descendant relationship. Most evolutionary changes in morphology occur in a short period of time relative to the total duration of species. After the descendant is established as a full species, there will be little evolutionary change except when the two species become sympatric for the first time.

These simple consequences of the allopatric theory can be combined into an expected pattern for the fossil record. Using stratigraphic, radiometric, or biostratigraphic criteria (for organisms other than those under study), we establish a regional framework of correlation. Starting with these correlations, patterns of geographic (not stratigraphic) variation among samples of fossils should appear. Tracing a fossil species through any local rock column, so long as no drastic changes occur in the physical environment, should produce *no* pattern of constant change, but one of oscillation in mean values. Closely

related (perhaps descendant) species that enter the rock column should appear suddenly and show no intergradation with the "ancestral" species in morphological features that act as inter-specific differentia. There should be no gradual divergence between the two species when both persist for some time to higher stratigraphic levels. Quite the contrary—it is likely that the two species will display their greatest difference when the descendant first appears. Finally, in exceptional circumstances, we may be able to identify the general area of the ancestor's geographic range in which the new species arose.

Another conclusion is that time and geography, as factors in evolution, are not so comparable as some authors have maintained (Sylvester-Bradley, 1951). The allopatric theory predicts that most variation will be found among samples drawn from different geographic areas rather than from different stratigraphic levels in the local rock column. The key factor is adjustment to a heterogeneous series of micro-environments vs. a general pattern of stasis through time.

In summary, we contrast the tenets and predictions of allopatric speciation with the corresponding statements of phyletic gradualism previously given:

(1) New species arise by the splitting of lineages.

(2) New species develop rapidly.

(3) A small sub-population of the ancestral form gives rise to the new species.

(4) The new species originates in a very small part of the ancestral species' geographic extent—in an isolated area at the periphery of the range.

These four statements again entail two important consequences:

(1) In any *local* section containing the ancestral species, the fossil record for the descendant's origin should consist of a sharp morphological break between the two forms. This break marks the migration of the descendant, from the peripherally isolated area in which it developed, into its ancestral range. Morphological change in the ancestor, even if directional in time, should bear no relationship to the descendant's morphology (which arose in response to local conditions in its isolated area). Since speciation occurs rapidly in small populations occupying small areas far from the center of ancestral abundance, we will rarely discover the actual event in the fossil record.

(2) Many breaks in the fossil record are real; they express the way in which evolution occurs, not the fragments of an imperfect record. The sharp break in a local column accurately records what happened in that area through time. Acceptance of this point would release us from a self-imposed status of inferiority among the evolutionary sciences. The paleontologist's gut-reaction is to view almost any anomaly as an artifact imposed by our institutional millstone—an imperfect fossil record. But just as we now tend to view the rarity of Precambrian metazoans as a true reflection of life's history rather than a testimony to the ravages of metamorphism or the lacunae of Lipalian

intervals, so also might we reassess the smaller breaks that permeate our Phanerozoic record. We suspect that this record is much better (or at least much richer in optimal cases) than tradition dictates.

Problems of phyletic gradualism. In our alternate picture of phyletic gradualism, we are not confronted with a self-contained theory from modern biology. The postulated mechanism for gradual uni-directional change is "orthoselection," usually viewed as a constant adjustment to a uni-directional change in one or more features of the physical environment. The concept of orthoselection arose as an attempt to remove the explanation of gradual morphological change from the realm of metaphysics ("orthogenesis"). It does *not* emanate from *Drosophila* laboratories, but represents a hypothetical extrapolation of selective mechanisms observed by geneticists.

Extrapolation of gradual change under selection to a complete model for the origin of species fails to recognize that speciation is primarily an ecological and geographic process. Natural selection, in the allopatric theory, involves adaptation to local conditions and the elaboration of isolating mechanisms. Phyletic gradualism is, in itself, an insufficient picture to explain the origin of diversity in the present, or any past, biota.

Although phyletic gradualism prevails as a picture for the origin of new species in paleontology, very few "classic" examples purport to document it. A few authors (MacGillavry, 1968, Eldredge, 1971) have offered a simple and literal interpretation of this situation: *in situ*, gradual, progressive evolutionary change is a rare phenomenon. But we usually explain the paucity of cases by a nearly-ritualized invocation of the inadequacy of the fossil record. It *is* valid to point out the rarity of thick, undisturbed, highly fossiliferous rock sections in which one or more species occur continuously throughout the sequence. Nevertheless, if most species evolved according to the tenets of phyletic gradualism, then, no matter how discontinuous a species' occurrence in thick sections, there should be a shift in one or more variables from sample to sample up the section. This is, in fact, the situation in most cases of postulated gradualism: the "gradualism" is represented by dashed lines connecting known samples. This procedure provides an excellent example of the role of preconceived pictures in "objectively documented" cases. One of the early "classics" of phyletic gradualism, Carruthers' (1910) study of the Carboniferous rugose coral *Zaphrentites delanouei* (Milne-Edwards and Haime) and its reinterpretation by Sylvester-Bradley (1951), is of this kind. We do not say that the analysis is incorrect; the *Z. delanouei* stock may have evolved as claimed. We merely wish to show how the *a priori* picture of phyletic gradualism has imposed itself upon limited data.

How pervasive, then, is gradualism in these quasi-continuous sequences? A number of authors (including, *inter alia*, Kurtén, 1965, MacGillavry, 1968, and Eldredge, 1971) have claimed that most species show little or no change throughout their stratigraphic range. But though it is tempting to conclude

that gradual, progressive morphological change is an illusion, we recognize that there is little hard evidence to support either view.

As a final, and admittedly extreme, example of *a priori* beliefs in phyletic gradualism, we cite the work of Brace (1967) on human evolution. This is all the more instructive since most paleoanthropologists, in reversing an older view that Brace still maintains, now claim that hominid evolution involves speciation by splitting as well as phyletic evolution by transformation (seen especially in the presumed coexistence of two australopithecine species in the African lower Pleistocene—Howell, 1967; Tobias, 1965; Pilbeam, 1968; Pilbeam and Simons, 1965). Brace (1967) has claimed that the fossil record of man includes four successive "stages" in direct ancestral-descendant relation. These are the Australopithecine (with two successive "phases"—the australopithecus and paranthropus), the Pithecanthropus, the Neanderthaloid, and, finally, the Modern Stage. In discussing the history of paleoanthropology, Brace shows that most denials of ancestral-descendant relationships among hominid fossils stem from a desire to avoid the conclusion that *Homo sapiens* evolved from some "lower," more "brutish" form. But Brace has lumped all such analyses under the catch phrase "hominid catastrophism." Hominid catastrophism, according to Brace, is the denial of ancestral-descendant relationships among fossils, with the invocation of extinction and subsequent migrations of new populations that arose by successive creation. Such views are, of course, absurd, but Brace would include *all* cladistic interpretations of the hominid record within "hominid catastrophism." To view hominid phylogeny as a gradual, progressive, unilineal process involving a series of stages, Brace claims, is the interpretation most consonant with evolutionary theory. His interpretation of phylogeny may be correct (though most experts deny it), but he is seriously wrong to claim that phyletic gradualism is the picture most consistent with modern biological thought. Quite apart from the issue of probable overlap in the ranges of his stages, it would be of great interest to determine the degree of stasis attained by them during any reasonably long period of time.

Application of allopatric concepts to paleontological examples. At this point, there is some justification for concluding that the picture of phyletic gradualism is poorly documented indeed, and that most analyses purporting to illustrate it directly from the fossil record are interpretations based on a preconceived idea. On the other hand, the alternative picture of stasis punctuated by episodic events of allopatric speciation rests on a few general statements in the literature and a wealth of informal data. The idea of *punctuated equilibria* is just as much a preconceived picture as that of phyletic gradualism. We readily admit our bias towards it and urge readers, in the ensuing discussion, to remember that our interpretations are as colored by our preconceptions as are the claims of the champions of phyletic gradualism by theirs. We merely reiterate: (1) that one must have some picture of speciation

in mind, (2) that the data of paleontology cannot decide which picture is more adequate, and (3) that the picture of punctuated equilibria is more in accord with the process of speciation as understood by modern evolutionists.

We could cite any number of reported sequences that fare better under notions of allopatric processes than under the interpretation of phyletic gradualism that was originally applied. This is surely true for all or part of the three warhorses of the English literature: horses themselves, the Cretaceous echinoid *Micraster*, and the Jurassic oyster *Gryphaea*. Simpson (1951) has shown that the phylogeny of horses is a luxuriant, branching bush, not the ladder to one toe and big teeth that earlier authors envisioned (Matthew and Chubb, 1921). Nichols (1959) believes that *Micraster senonensis* was a migrant from elsewhere and that it did not arise and diverge gradually from *M. cortestudinarium* as Rowe (1899) had maintained. Hallam (1959, 1962) has argued that the transition from *Liostrea* to *Gryphaea* was abrupt and that *neither* genus shows *any* progressive change through the basal Liassic zones, contrary to Trueman's claim (1922, p. 258) that: "It is doubtful whether any better example of lineage of fossil forms could be found." Gould (1971b and in press) has confirmed Hallam's conclusions. Hallam interprets the sudden appearance of *Gryphaea* as the first entry into a local rock column of a species that had evolved rapidly elsewhere. He writes (1962, p. 574): "This interpretation is more in accord with the experience of most invertebrate paleontologists who, despite continued collecting all over the world and an ever-increasing amount of research, find 'cryptogenic' genera and species far more commonly than they detect gradual trends or lineages. The sort of evolution I tentatively propose for *Gryphaea* could in fact be quite normal among the invertebrates." We agree.

We choose, rather, to present two examples from our own work which we believe are interpreted best from the viewpoint of allopatric speciation. We prefer to emphasize our own work simply because we are most familiar with it and are naturally more inclined to defend our interpretations.

Gould (1969) has analyzed the evolution of *Poecilozonites bermudensis zonatus* Verrill, a pulmonate snail, during the last 300,000 years of the Bermudian Pleistocene. The specimens were collected from an alternating sequence of wind-blown sands and red soils. Formational names, dominant lithologies, and glacial-interglacial correlations are given in *table 5–1*.

The small area and striking differentiation of stratigraphic units in the Bermudian Pleistocene permit a high degree of geographic and temporal control. *P. bermudensis* (Pfeiffer) is plentiful in all post-Belmont formations; in addition, one subspecies, *P.b. bermudensis*, is extant and available for study in the laboratory.

Distinct patterns of color banding differentiate an eastern from a western population of *P. bermudensis zonatus*. The boundary between these two groups is sharp, and there are no unambiguous cases of introgression. *P.*

bermudensis zonatus was divided into two stocks, evolving in parallel with little gene flow between them, throughout the entire interval of Shore Hills to Southampton time. Both eastern and western *P.b. zonatus* became extinct sometime after the deposition of Southampton dunes; they were replaced by *P.b. bermudensis*, a derivative of eastern *P.b. zonatus* which had been evolving separately in the area of St. George's Island since St. George's time. Gould (1969, 1970b) has discussed the parallel oscillation of several morphological features in both stocks of *P.b. zonatus*; these are adaptive shifts in response to glacially-controlled variations in climate. Both stocks exhibit stability in other features that serve to distinguish them from their nearest relatives. There is no evidence for any gradual divergence between eastern and western *P.b. zonatus*.

Several samples of *P. bermudensis* share many features that distinguish them from *P. bermudensis zonatus*. These characters can be arranged in four categories: color, general form of the spire, thickness of the shell, and shape of the apertural lip. The ontogeny of *P.b. zonatus* illustrates the interrelation of these categories. Immature shells of *P.b. zonatus* are weakly colored, relatively wide, lack a callus, and have the lowest portion of the outer apertural lip at the umbilical border. This combination of character states is exactly repeated in the large *mature* shells of non-*zonatus* samples of *P. bermudensis*. Since every ontogenetic feature developed at or after the fifth whorl in non-*zonatus* samples is attained by whorls 3–4 in *P.b. zonatus*, Gould (1969) concludes that the non-*zonatus* samples of *P. bermudensis* are derived by paedomorphosis from *P.b. zonatus*.

These paedomorphic samples range through the entire interval of Shore Hills to Recent. The most obvious hypothesis would hold that they constitute a continuous lineage evolving separately from *P.b. zonatus*. Gould rejects this and concludes that paedomorphic offshoots arose from the *P.b. zonatus* stock at four different times; the arguments are based on details of stratigraphic and geographic distrubution, as well as on morphology.

Figure 5–4 summarizes the history of splitting in the *P.b. zonatus* lineage. The earliest paedomorph, *P.b. fasolti* Gould, occurs in the Shore Hills Formation within the geographic range of eastern *P.b. zonatus*. *P.b. fasolti* and the contemporary population of eastern *P.b. zonatus* share a unique set of morphological features including, *inter alia*, small size at any given whorl, low spire, relatively wide shell, and a wide umbilicus. These features unite the Shore Hills paedomorph and non-paedomorph, and set them apart from all post-Shore Hills *P. bermudensis*.

In the succeeding Harrington Formation, paedomorphic samples of *P. bermudensis* lived in both the eastern and western geographic regions of *P.b. zonatus*. The eastern paedomorph, *P.b. sieglindae* Gould, may have evolved from the Shore Hills paedomorph, *P.b. fasolti*. However, both *P.b. sieglindae*

Table 5–1. Stratigraphic column of Bermuda.

Formation	*Description*	*Interpretation*
Recent	Poorly developed brownish soil or crust	Interglacial
Southampton	Complex of eolianites and discontinuous unindurated zones	„
St. George's	Red paleosol of island wide extent	Glacial
Spencer's Point	Intertidal marine, beach and dune facies	Interglacial
Pembroke	Extensive eolianites and discontinuous unindurated zones	„
Harrington	Fairly continuous unindurated layer with shallow water marine and beach facies	„
Devonshire	Intertidal marine and poorly developed dune facies	„
Shore Hills	Well-developed red paleosol of island-wide extent	Glacial
Belmont	Complex shallow water marine, beach and dune facies	Interglacial
Soil (?)	A reddened surface rarely seen in the Walsingham district	Glacial?
Walsingham	Highly altered elolianites	Interglacial

and the contemporaneous population of eastern *P.b. zonatus* lack the distinctive features of all Shore Hills *P. bermudensis* and a more likely hypothesis holds that the features uniting all post-Shore Hills *P. bermudensis* were evolved only once. If this is the case, *P.b. sieglindae* is a second paedomorphic derivative of eastern *P.b. zonatus*.

P.b. sieglindae differs from its contemporary paedomorph *P.b. siegmundi* Gould in that each displays the color pattern of the local non-paedomorph. Very simply, *P.b. sieglindae* is found in eastern Bermuda and shares the banding pattern of eastern *P.b. zonatus*, while *P.b. siegmundi* is found in western Bermuda and has the same color pattern as western *P.b. zonatus*. In addition, both *P.b. sieglindae* and *P.b. siegmundi* evolved at the periphery of the known range of their putative ancestors. The independent derivation of the two Harrington paedomorphs from the two stocks of *P.b. zonatus* seems clear.

Finally, the living paedomorph, *P.b. bermudensis*, first appears in the St. George's Formation on St. George's Island. While St. George's Island is within the geographic range of eastern *P.b. zonatus*, it is far removed from the

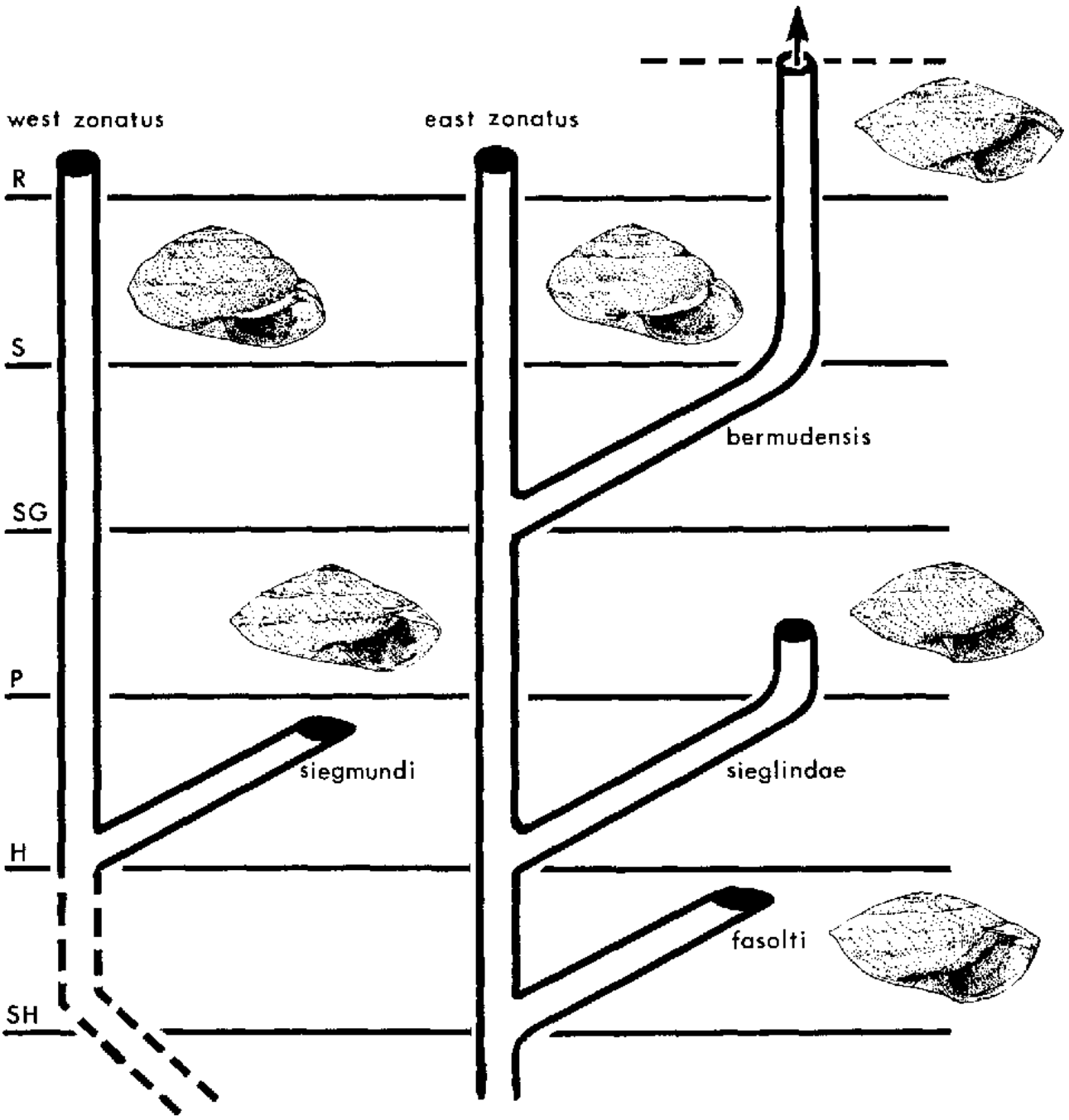

Figure 5–4: Reconstruction of the phylogenetic history of *P. bermudensis* showing iterative development of paedomorphic subspecies. SH—Shore Hills; H—Harrington; P—Pembroke; SG—St. George's; S—Southampton; R—Recent. From Gould, 1969; figure 20.

area in which *P.b. sieglindae* arose and lived. Gould concludes that *P.b. sieglindae* was a short-lived population that never enjoyed a wide geographic distribution; he estimates that the Pembroke population's range did not exceed 200 meters. Although there is little morphological evidence to support it, Gould recognizes a fourth paedomorphic subspecies, *P.b. bermudensis*, derived directly from (eastern) *P.b. zonatus*. The conclusion is based upon geographic and stratigraphic data.

Gould (1969) has advanced an adaptive explanation for the four separate origins of paedomorphic populations from *P.b. zonatus*. This explanation, based on the value of thin shells in lime-poor soils, need not be elaborated here. What is important, for our purposes, is to emphasize that the reconstruction of phylogenetic histories for the paedomorphs involves (1) attention to geographic data (the allopatric model), (2) discontinuous stratigraphic occurrence (a more literal interpretation of the fossil record), and (3) formal arguments based on morphology. It is entirely possible, from morphological data alone, to interpret the three paedomorphs of the eastern *zonatus* area as a gradational biostratigraphic series. *Figure 5–5* shows a tempting interpretation of phyletic gradualism for "lower eccentricity," an apertural

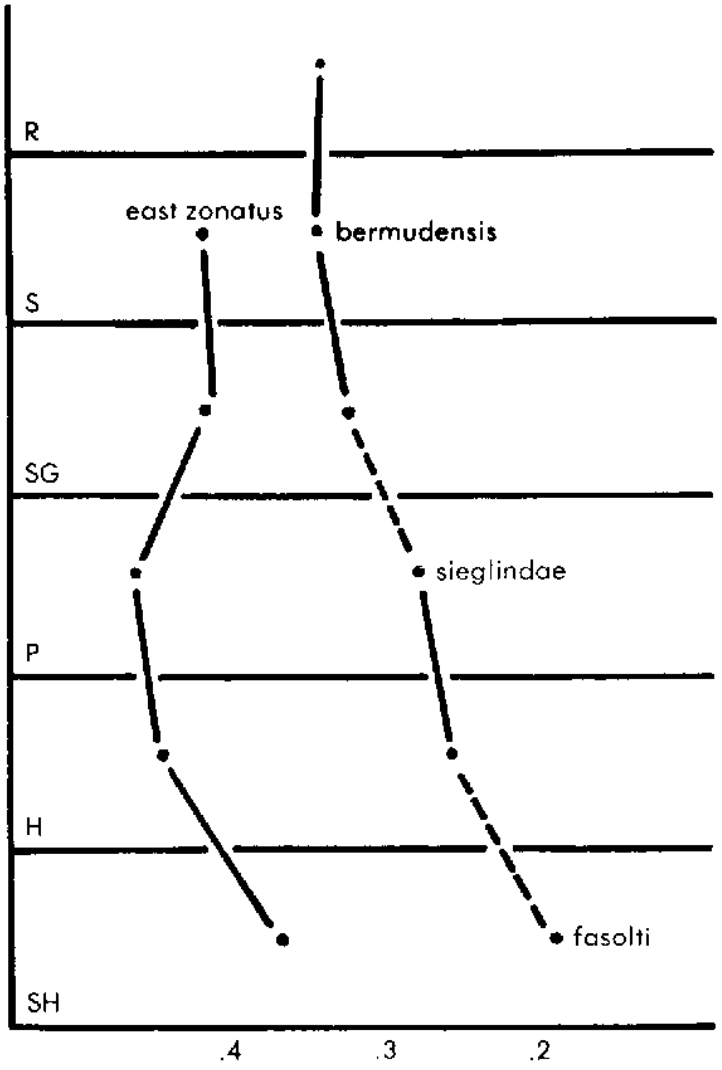

Figure 5–5: Plot of means of mean sample values of "lower eccentricity" in *P. bermudensis*. Dashed lines show the phylogeny of the three paedomorphs of eastern *zonatus* as a direct ancestral-descendant sequence, and offer a tempting instance of phyletic gradualism. Abbreviations as in *figure 5–4*.

variable. Values gradually increase through time. *Figure 5–6*, however, confounds this interpretation by showing that stratigraphic variability in "differential growth ratio" within both *P.b. sieglindae* and *P.b. bermudensis* varies in a direction *opposite* to the net stratigraphic "trend": *P.b. fasolti—P.b. sieglindae—P.b. bermudensis*: this could be read to indicate that each subspecies is unique. In fact, neither graph affords sufficient evidence to warrant either conclusion. Morphology, stratigraphy, and geography must all be evaluated.

The phylogenetic history of the trilobite *Phacops rana* (Green) from the Middle Devonian of North America (Eldredge, 1971; 1972) provides another example of the postulated operation of allopatric processes. As in *Poecilozonites bermudensis*, full genetic isolation was probably not established between "parent" and "daughter" taxa; this conclusion, based on

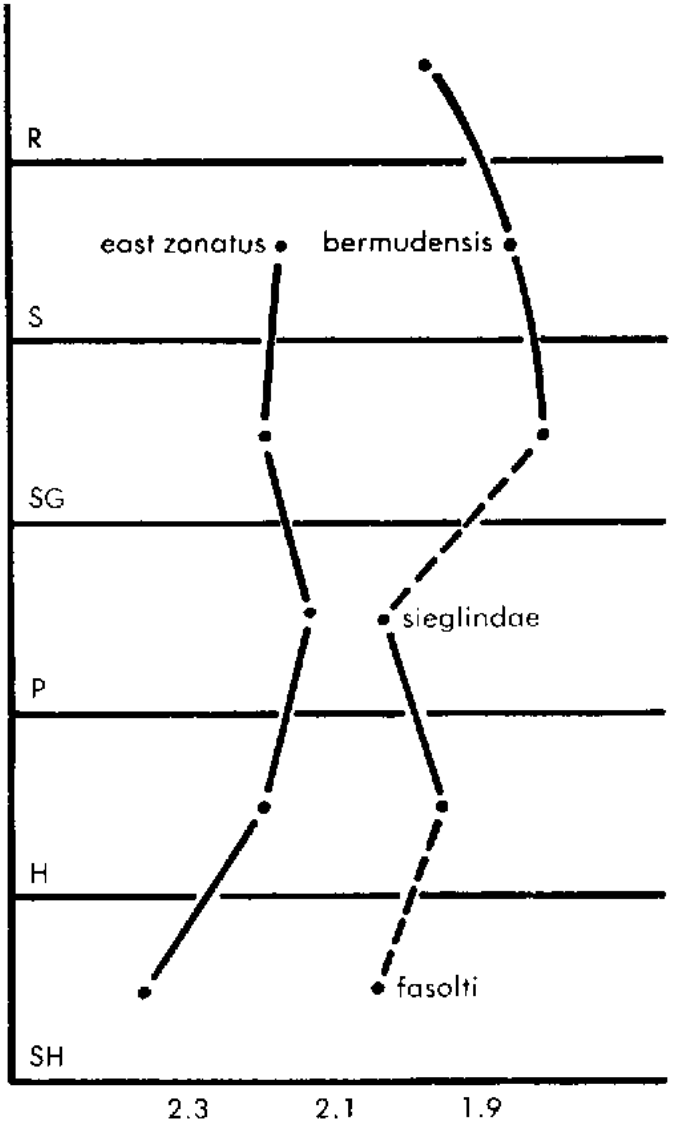

Figure 5–6: Plot of means of mean sample values for "differential growth ratio" in *P. bermudensis*. Dashed lines show the interpretation of the phylogeny of the three paedomorphs as a direct ancestral-descendant sequence. Abbreviations as in *figure 5–4*.

inferences from morphological variability, may be unwarranted. For our purposes, it does not matter whether we are dealing with four subspecies of *P. rana*, or four separate species of *Phacops*, including *P. rana* and its three closest relatives. The basic mode of evolution underlying the group's phylogenetic history as a whole is the same in either case.

Features of eye morphology exhibit the greatest amount of variation among samples of *P. rana*. Lenses are arranged on the visual surface of the eye in vertical dorso-ventral files (Clarkson, 1966). A stable number of dorso-ventral files, characteristic of the entire sample in any population, is reached early in ontogeny. The number of dorso-ventral (d.-v.) files is the most important feature of interpopulational variation in *P. rana*.

The closest known relative of *P. rana* is *P. schlotheimi* (Bronn) *s. l.*, from the Eifelian of Europe and Africa; this group has recently been revised by C. J. Burton (1969). In addition, several samples of *P. rana* have been found in the Spanish Sahara in northwestern Africa (Burton and Eldredge, in preparation). *P. schlotheimi* and the African specimens of *P. rana* are most similar to *P. rana milleri* Stewart and *P. rana crassituberculata* Stumm, the two oldest subspecies of *P. rana* in North America. All these taxa possess 18 dorso-ventral files. Eldredge (1972) concludes that 18 is the primitive number of d.-v. files for all North American *Phacops rana*.

Figure 5–7 summarizes relationships among the four subspecies of *P. rana* without regard to stratigraphic occurrence. The oldest North American *P. rana* occurs in the Lower Cazenovian Stage of Ohio and central New York State. All have 18 d.-v. files. Populations with 18 d.-v. files (*P. rana milleri* and *P. rana crassituberculata*) persist into the Upper Cazenovian Stage in the epicontinental seas west of the marginal basin in New York and the Appalachians.

Of the two samples the one that displays intra-populational variation in d.-v. file number occurs in the Lower Cazenovian of central New York. Some specimens have 18 d.-v. files, while others reduce the first d.-v. file to various degrees; a few lack it altogether. *All P. rana* from subsequent, younger horizons in New York and adjacent Appalachian states have 17 dorso-ventral files. Apparently, 17 d.-v. file *P. rana rana* arose from an 18 d.-v. file population on the northeastern periphery of the Cazenovian geographic range of *P. rana*. Seventeen d.-v. file *P. rana* persist, unchanged in most respects, through the Upper Cazenovian, Tioughniogan, and Taghanic Stages in the eastern marginal basin. Seventeen d.-v. file *P. rana rana* first appears in the shallow interior seas at the beginning of the Tioughniogan Stage, replacing the 18 d.-v. file populations that apparently became extinct during a general withdrawal of seas from the continental interior. All Tioughniogan *P. rana* possess 17 dorso-ventral files.

A second, similar event involving reduction in dorso-ventral files occurred during the Taghanic. Here again, a variable population inhabited the eastern

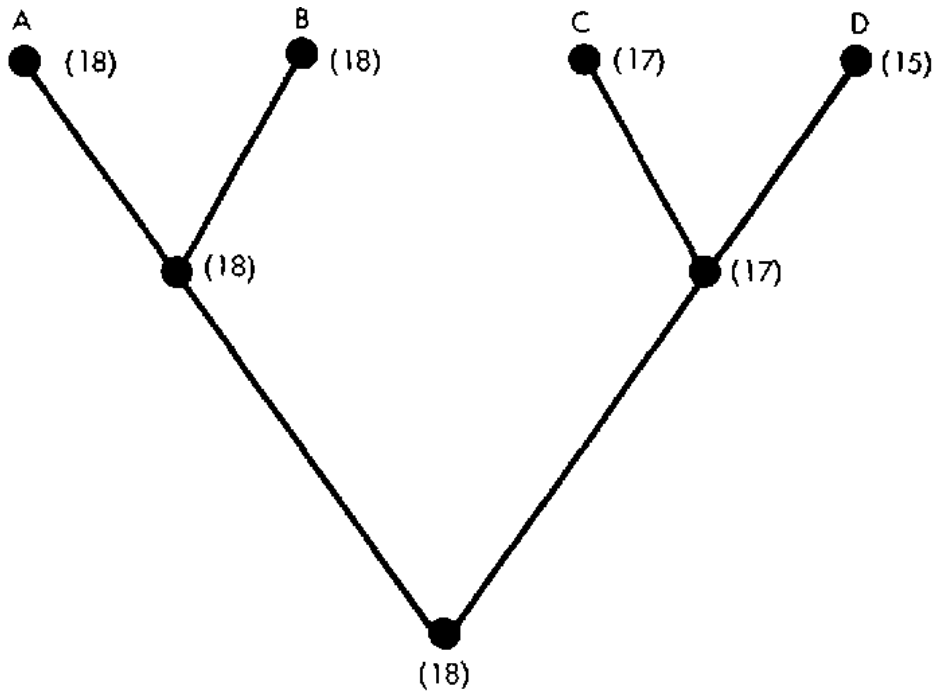

Figure 5–7: Outline of relationships of four subspecies of *Phacops rana*. A—*Phacops rana crassituberculata* Stumm; B—*Phacops rana milleri* Stewart; C—*Phacops rana rana* (Green); D—*Phacops rana norwoodensis* Stumm. Numbers in parentheses refer to number of dorso-ventral files typical of subspecies or hypothesized to characterize condition of common ancestor.

marginal basin in New York. This suggests that, once more, reduction in d.-v. files occurred allopatrically on the periphery of the known range of *P. rana rana*. The subsequent spread of stabilized, 15 d.-v. file *P. rana norwoodensis* through the Taghanic seas of the continental interior was instantaneous in terms of our biostratigraphic resolution. *Figure 5–8* summarizes this interpretation of the history of *P. rana*.

Under the tenets of phyletic gradualism, this story has a different (and incorrect) interpretation: the three successional taxa of the epeiric seas form an *in situ* sequence of gradual evolutionary modification. The sudden transitions from one form to the next are the artifact of a woefully incomplete fossil record. Most evolutionary change occurred during these missing intervals: fill in the lost pieces with an even dotted line.

If the interpreter pays attention to geographic detail, however, quite a different tale emerges, one that allows a more literal reading of the fossil record. Now the story is one of stasis: no variation in the most important feature of discrimination (number of d.-v. files—actually a complex of highly interrelated variables) through long spans of time. Two samples displaying intra-populational variation in numbers of d.-v. files identify relatively "sudden" events of reduction in files on the periphery of the species' geographic range. These two samples, moreover, have a very short stratigraphic, and very restricted geographic, distribution.

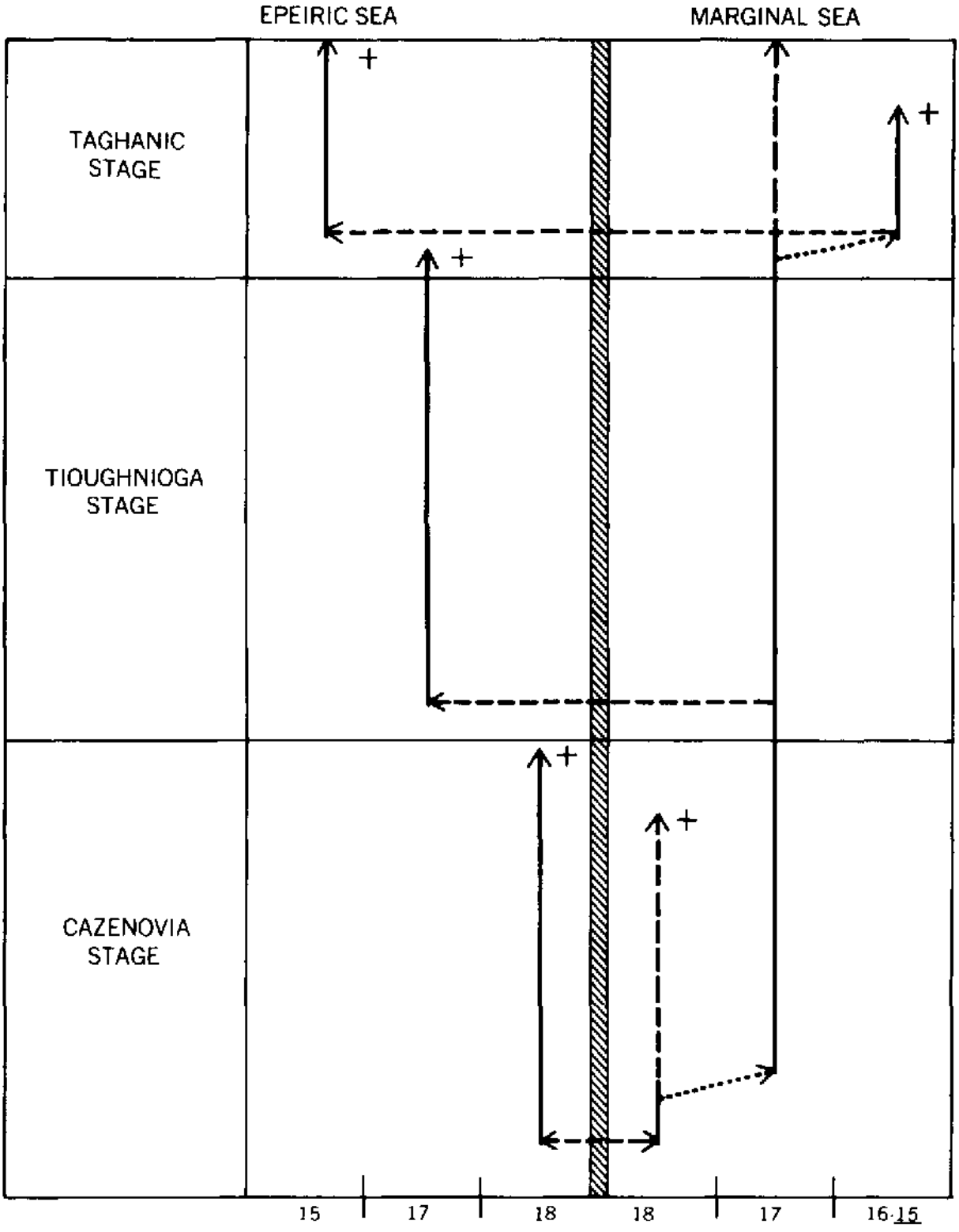

Figure 5–8: Hypothesized phylogeny of the *Phacops rana* stock in the Middle Devonian of North America. Numbers at the base of the diagram refer to the population number of dorso-ventral files. Dotted lines: origin of new (reduced) number of d.-v. files in a peripheral isolate; horizontal dashed lines: migration; vertical solid lines: presence of taxon in indicated area; dashed vertical lines: persistence of ancestral stock in a portion of the marginal sea other than that in which the derived taxon occurs. Crosses denote final disappearance; for fuller explanation, see text.

Our two examples, so widely separated in scale, age, and subject, have much in common as exemplars of allopatric processes. Both required an attention to details of *geographic* distribution for their elucidation. Both involved a *more literal* reading of the fossil record than is allowed under the unconscious guidance of phyletic gradualism. Both are characterized by *rapid* evolutionary events punctuating a history of stasis. These are among the expected consequences if most fossil species arose by allopatric speciation in small, peripherally isolated populations. This alternative picture merely represents the application to the fossil record of the dominant theory of speciation in modern evolutionary thought. We believe that the consequences of this theory are more nearly demonstrated than those of phyletic gradualism by the fossil record of the vast majority of Metazoa.

Some Extrapolations to Macroevolution

Before 1930, paleontology sought a separate theory for the causes of macroevolution. The processes of microevolution (including the origin of species) were deemed insufficient to generate the complexity and diversity of life, even under the generous constraint of geological time; a variety of special causes were proposed—vitalism, orthogenesis, racial "life" cycles, and universal acceleration in development to name just a few.

However, the advent of the "modern synthesis" inspired a reassessment that must stand as the major conceptual advance in 20th-century paleontology. Special explanations for macroevolution were abandoned for a simplifying theory of extrapolation from species-level processes. All evolutionary events, including those that seemed most strongly "directed" and greatly extended in time, were explained as consequences of mutation, recombination, selection, etc.—i.e., as consequences only of the phenomena that produce evolution in nature's real taxon, the species. (The modern synthesis received its name because it gathered under one theory—with population genetics at its core—the events in many subfields that had previously been explained by special theories unique to that discipline. Such an occurrence marks scientific "progress" in its truest sense—the replacement of special explanations carrying little power in prediction or extension with general theories, rich in implications and capable of unifying a diverse set of phenomena that had seemed unrelated. Thus Simpson (1944, 1953) did for paleontology what Dobzhansky (1937) had done for classical genetics, Mayr (1942) for systematics, de Beer (1940) for development, White (1954) for cytology, and Stebbins (1950) for systematic botany—he exemplified the phenomena of his field as the result of Darwinian processes acting upon species.)

We have discussed two pictures for the origin of species in paleontology. In the perspective of a species-extrapolation theory of macroevolution, we

should now extend these pictures to see how macroevolution proceeds under their guidance. If actual events, as recorded by fossils, fit more comfortably with the predictions of either picture, this will be a further argument for that picture's greater adequacy.

Under phyletic gradualism, the history of life should be one of *stately unfolding*. Most changes occur slowly and evenly by phyletic transformation; splitting, when it occurs, produces a slow and very gradual divergence of forms (Weller's (1969) tree of life—reproduced as *figure 5–9*—records the extrapolation of this partisan view, not a neutral hatrack for the fossils themselves). We have already named our alternate picture for its predicted extrapolation—*punctuated equilibria*. The theory of allopatric speciation implies

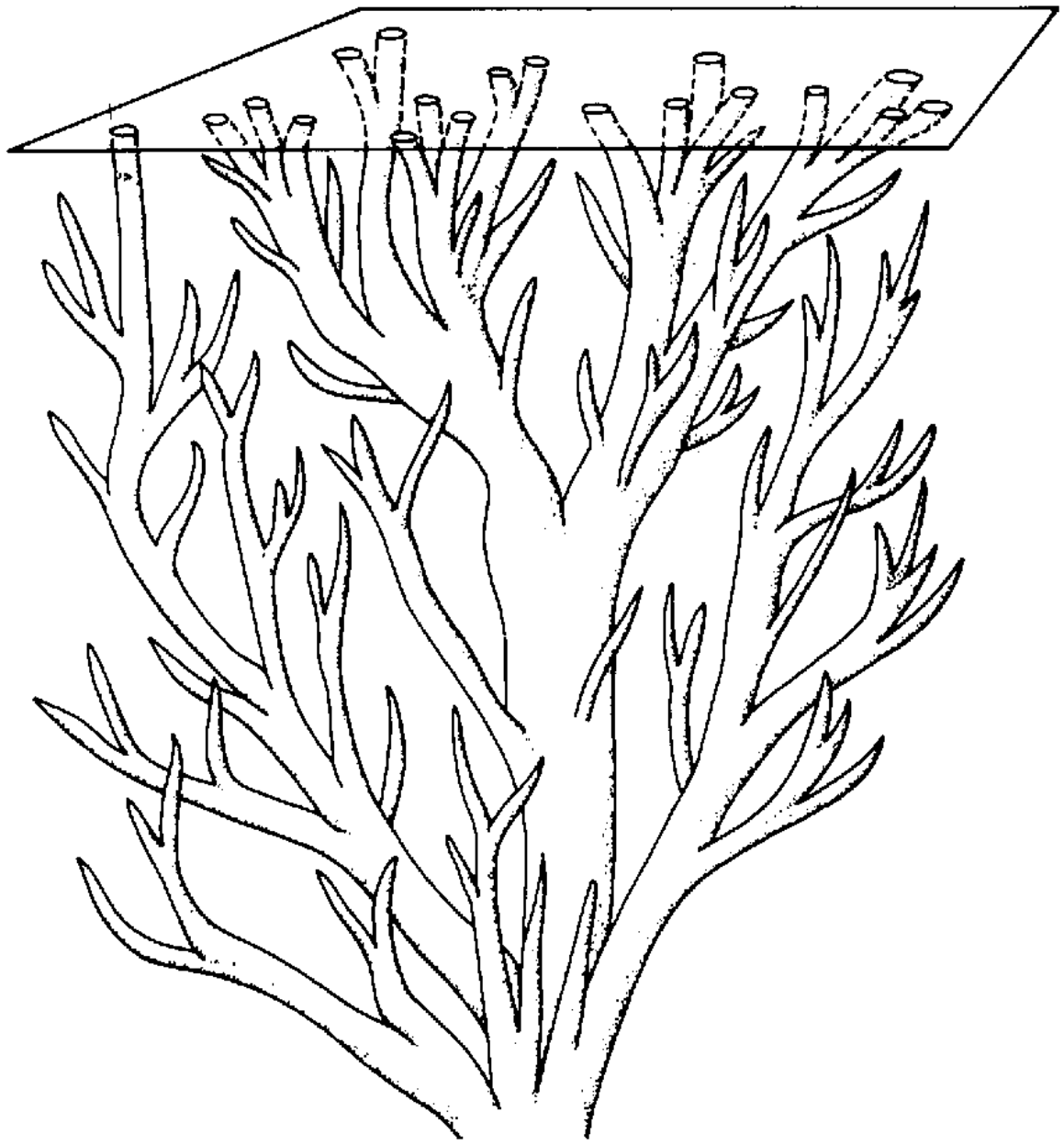

Figure 5–9: The "Tree of Life" viewed from the perspective of phyletic gradualism. Branches diverge gradually one from the other. A slow and relatively equal rate of evolution pervades the system. From Weller, 1969; figure 637.

that a lineage's history includes long periods of morphologic stability, punctuated here and there by rapid events of speciation in isolated subpopulations.

We now consider two phenomena of macroevolution as case studies of our extrapolated pictures. The first is widely recognized as anomalous under the unconscious guidance of stately unfolding; it emerges as an expectation under the notion of punctuated equilibria. The second phenomenon seems, superficially, to have an easier explanation under stately unfolding, but we shall argue that it has a more interesting interpretation when viewed with the picture of punctuated equilibria.

(1) *"Classes" of great number and low diversity*

To many paleontologists, nothing is more distressing than the current situation in echinoderm systematics. Ubaghs (1967), in his contribution to the *Treatise on Invertebrate Paleontology*, recognizes 20 classes and at least one has been added since then—Robison and Sprinkle's (1969) ctenocystoids. Yet, although all appeared by the Ordovician, only five survived the Devonian. Moreover, although each class has a distinct Bauplan, many display a diversity often considered embarrassingly small for so exalted a taxonomic rank—the *Treatise* describes eight classes with five or fewer genera; five of these include but a single genus (as does the new ctenocystoids).

There are two aspects to this tale that fit poorly with the traditional view of stately unfolding:

(1) The presence of 21 classes by the Ordovician, coupled with their presumed monophyletic descent, requires extrapolation to a common ancestor uncomfortably far back in the Precambrian if Ordovician diversity is the apex of a gradual unfolding. Yet current views of Precambrian evolution will not happily accommodate a complex metazoan so early (Cloud, 1968).

(2) We expect that successively higher ranks of the taxonomic hierarchy will contain more and more taxa: a class with one genus is anomalous and we are led either to desperate hopes for synonymy or, once again, to our old assumption—that we possess a fragmentary record of a truly diverse group. Yet this expectation is no consequence of the logic of taxonomy (which demands only that each taxon be *as* inclusive as the lower ones it incorporates); it arises, rather, from a picture of stately unfolding. In *figure 5–9*, a new higher taxon attains its rank *by virtue of* its diversity—an evenly progressing, evenly diverging set of branches cannot produce such a taxon with limited diversity, for a lineage "graduates" from family to order to class only as it persists to a tolerable age and branches an acceptable number of times.

With the picture of punctuated equilibria, however, classes of small membership are welcome and echinoderm evolution becomes more intriguing than bothersome. Since speciation is rapid and episodic, repeated splitting during short intervals is likely when opportunities for full speciation following isolation are good (limited dangers of predation or competition in peripheral

environments, for example—a likely Lower Cambrian situation). When these repeated splits affect a small, isolated lineage; when adaptation to peripheral environments involves new modes of feeding, protection, and locomotion; and when extinction of parental species commonly follows the migration of descendants to the ancestral area, then very distinct phenons with few species will develop. Since higher taxa are all "arbitrary" (they reflect no interacting group in nature, but rather a convenient arrangement of species that violates no rule of monophyly, hierarchical ordering, etc.), we believe that they should be defined by morphology. Criteria of diversity are too closely tied to partisan pictures; morphology, though not as "objective" as some numerical taxonomists claim, is at least more functional for information retrieval.

(2) *Trends*

Trends, or biostratigraphic character gradients, are frequently mentioned as basic features of the fossil record. Sequences of fossils, said to display trends, range from the infraspecific through the very highest levels of the taxonomic hierarchy. Trends at and below the species level were discussed in the previous section, but the relation between phyletic gradualism and trends among related clusters of species—families or orders—remains to be examined.

Many, if not most, trends involving higher taxa may simply reflect a selective rendering of elements in the fossil record, chosen because they seem to form a morphologically-graded series coincident with a progressive biostratigraphic distribution. In this sense, trends may represent simple extrapolations of phyletic gradualism.

But a claim that all documented trends are just unwarranted extrapolations based on a preconception would be altogether too facile an explanation for the large numbers of trends cited in the literature. For this discussion, we accept trends as a real and important phenomenon in evolution, and adopt the simple definition given by MacGillavry (1968, p. 72): "A trend is a direction which involves the *majority* of related lineages of a group" (our italics).

If trends are real and common, how can they be reconciled with our picture, in which speciation occurs in peripheral isolates by adaptation to local conditions and the perfection of isolating mechanisms? The problem may be stated in another way: Sewall Wright (1967, p. 120) has suggested that, just as mutations are stochastic with respect to selection within a population, so might speciation be stochastic with respect to the origin of higher taxa. As a slight extension of that statement, we might claim that adaptations to local conditions by peripheral isolates are stochastic with respect to long-term, net directional change (trends) within a higher taxon as a whole. We are left with a bit of a paradox: to picture speciation as an allopatric phenomenon, involving rapid differentiation within a general, long-term picture of stasis, is to

deny the picture of directed gradualism in speciation. Yet, superficially at least, this directed gradualism is easier to reconcile with valid cases of long-term trends involving many species.

MacGillavry's definition of a trend removes part of the problem by using the expression "majority of related lineages." This frees us from the constraint of reconciling *all* events of adaptation to local conditions in peripheral isolates, with long-term, net directional change.

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 in the case of selection upon mutations, the initial variations would be stochastic with respect to this change (*figure 5–10*). We postulate no "new" type of selection. We simply state a view of long-term, superficially "directed" phenomena that is in accord with the theory of allopatric speciation, and also avoids the largely untestable concept of orthoselection.

Conclusion: Evolution, Stately or Episodic?

Heretofore, we have spoken of the morphological stability of species in time without examining the reasons for it. The standard definition of a biospecies—as a group of actually or potentially reproducing organisms sharing a common gene pool—specifies the major reason usually cited: gene flow. Since the subpopulations of a species adapt to a range of differing local environments, we might expect these groups to differentiate, acquire isolating mechanisms and, eventually, to form new species. But gene flow exerts a homogenizing influence "to counteract local ecotypic adaptation by breaking up well-integrated gene complexes" (Mayr, 1963, p. 178). The role of gene flow is recognized in the central tenet of allopatric speciation: speciation occurs in *peripheral* isolates because only geographic separation from the parental species can reduce gene flow sufficiently to allow local differentiation to proceed to full speciation.

Recently, however, a serious challenge to the importance of gene flow in species' cohesion has come from several sources (Ehrlich and Raven, 1969, for example). Critics claim that, in most cases, gene flow is simply too restricted to exert a homogenizing influence and prevent differentiation. This

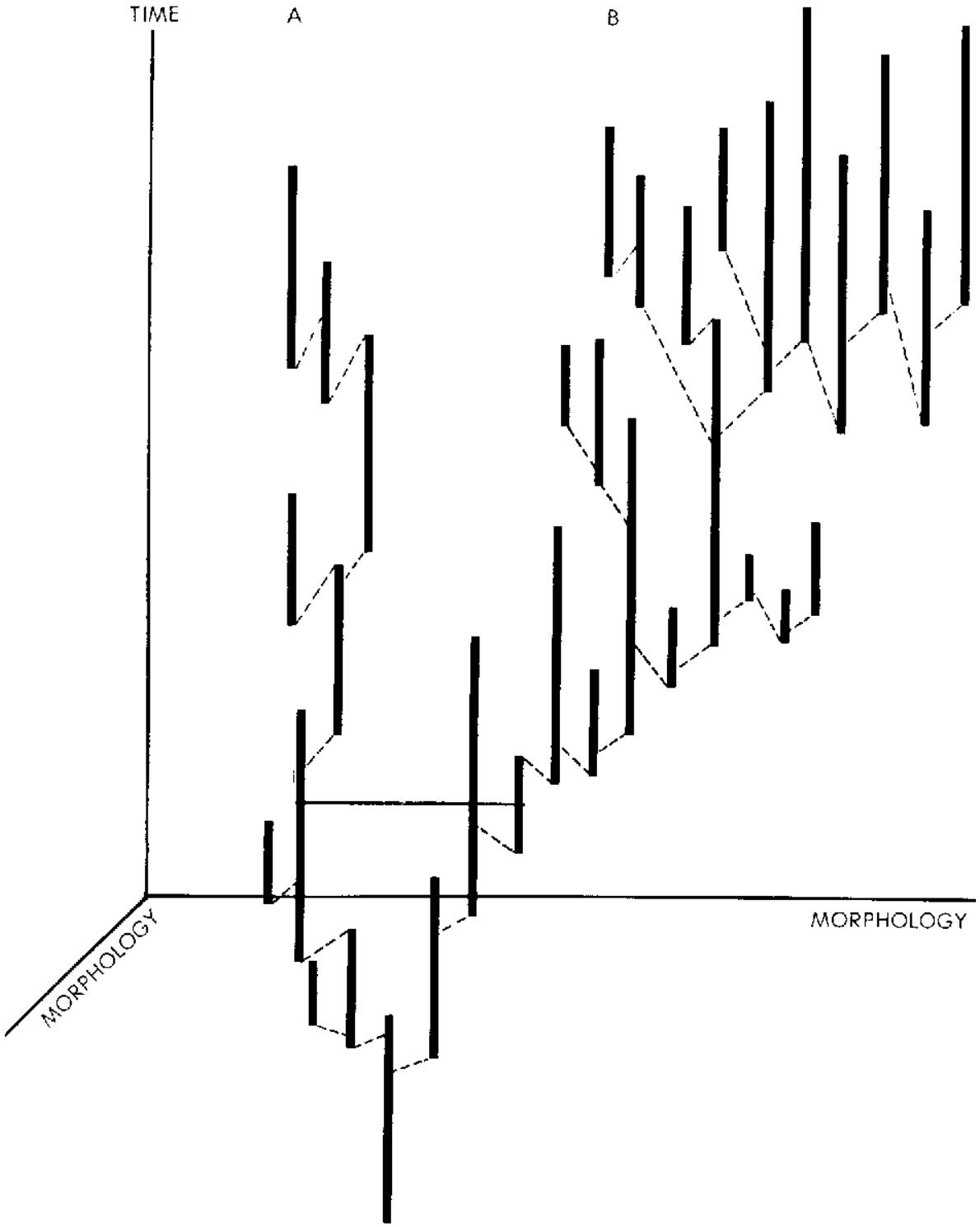

Figure 5–10: Three-dimensional sketch contrasting a pattern of relative stability (A) with a trend (B), where speciation (dashed lines) is occurring in both major lineages. Morphological change is depicted here along the horizontal axes, while the vertical axis is time. Though a retrospective pattern of directional selection might be fitted as a straight line in (B), the actual pattern is stasis within species, and differential success of species exhibiting morphological change in a particular direction. For further explanation, see text.

produces a paradox: why, then, are species coherent (or even recognizable)? Why do groups of (relatively independent) local populations continue to display a fairly consistent phenotype that permits their recognition as a species? Why does reproductive isolation not arise in every local population? Why is the local population itself not considered the "real" unit in evolution (as some would prefer—Sokal and Crovello, 1970, p. 151, for example)?

The answer probably lies in a view of species and individuals as homeostatic systems—as amazingly well-buffered to resist change and maintain stability in the face of disturbing influences. This concept has been urged particularly by Lerner (1954) and Mayr (1963), though the latter still gives more weight to gene flow than many will allow. Lerner (1954, p. 6) recognizes two types of homeostasis, mediated in both cases, he believes, by the generally higher fitness of heterozygous vs. homozygous genotypes: (1) ontogenetic self-regulation (developmental homeostasis) "based on the greater ability of the heterozygote to stay within the norms of canalized development" and (2) self-regulation of populations (genetic homeostasis) "based on natural selection favoring intermediate rather than extreme phenotypes." In this view, the importance of peripheral isolates lies in their small size and the alien environment beyond the species border that they inhabit—for only here are selective pressures strong enough and the inertia of large numbers sufficiently reduced to produce the "genetic revolution" (Mayr, 1963, p. 533) that overcomes homeostasis. The coherence of a species, therefore, is not maintained by interaction among its members (gene flow). It emerges, rather, as an historical consequence of the species' origin as a peripherally isolated population that acquired its own powerful homeostatic system. (We regard this idea as a serious challenge to the conventional view of species' reality that depends upon the organization of species as ecological units of *interacting* individuals in nature. If groups of nearly-independent local populations are recognized as species only because they share a set of homeostatic mechanisms developed long ago in a peripheral isolate that was "real" in our conventional sense of interaction, then some persistent anomalies are resolved. The arrangement of many asexual groups into good phenetic "species," quite inexplicable in interaction is the basis for coherence, receives a comfortable explanation under notions of homeostasis.)

Thus, the challenge to gene flow that seemed to question the stability of species in time ends by reinforcing that stability even more strongly. If we view a species as a set of subpopulations, all ready and able to differentiate but held in check only by the rein of gene flow, then the stability of species is a tenuous thing indeed. But if that stability is an inherent property both of individual development and the genetic structure of populations, then its power is immeasurably enhanced, for the basic property of homeostatic systems, of steady states, is that they resist change by self-regulation. That local popula

tions do not differentiate into species, even though no external bar prevents it, stands as strong testimony to the inherent stability of species in time.

Paleontologists should recognize that much of their thought is conditioned by a peculiar perspective that they must bring to the study of life: they must look down from its present complexity and diversity into the past: their view must be retrospective. From this vantage point, it is very difficult to view evolution as anything but an easy and inevitable result of mere existence, as something that unfolds in a natural and orderly fashion. Yet we urge a different view. The norm for a species or, by extension, a community is stability. Speciation is a rare and difficult event that punctuates a system in homeostatic equilibrium. That so uncommon an event should have produced such a wondrous array of living and fossil forms can only give strength to an old idea: paleontology deals with a phenomenon that belongs to it alone among the evolutionary sciences and that enlightens all its conclusions—time.