

The process of speciation and interpretation of the fossil record

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Most recent discussions of the implications of the New Systematics for paleontology have involved the practicality, or operationality, of applying the bio-species concept in recognizing and naming fossil taxa. Relatively little attention has been paid to the theoretical consequences that modern population biology and allopatric speciation theory should have for the interpretation of the fossil record.

In enumerating some of these consequences which seem to us to be relevant to a more correct interpretation of paleontological data, it is first necessary to emphasize that mechanisms operative in the speciation process can be studied directly only with experimental and field observational techniques with living organisms. No mechanistic theory can be generated directly from paleontological data. Instead, general theories of biological processes advanced by students of the Recent biota inherently possess general consequences which may be called "patterns." On the basis of these predicted patterns, 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 consonant with the retrodicted consequences (expected patterns) of a particular theory of speciation? We can apply and test, but in no sense can we generate fresh mechanisms. If minor, but consistent, discrepancies are found between paleontological data and the expected patterns, paleontologists may be able to suggest certain aspects of a general theory which could stand improvement. But again, we are incapable of formulating these improvements ourselves. Rates and directions of morphological change over long periods of time are perhaps the more obvious examples of aspects of evolutionary patterns which a paleontologist can test against prediction based on processes observed over short periods of time by neontologists.

Within the last thirty years, the allopatric theory of speciation

has gained ascendancy to the point where the vast majority of biologists view it as the theory of speciation, at least among the Metazoa. Its only serious challenger is the sympatric^g_N theory. Both "pictures" depict speciation as a splitting of lineages; in fact, for most biologists, speciation is synonymous with splitting. The third picture available to us, and already alluded to above, is one of phyletic gradualism, where new species are thought to originate merely by the inexorable passage of time with a concomitantly constant, uni-directional change in morphology. This is the predominant model underlying paleontological analyses of phylogeny. When splitting is considered by paleontologists, it is pictured, usually rather vaguely, as a simple dichotomization of a phylogenetic lineage, whose branches diverge gradually through time.

It follows from the previous discussion that paleontological data ^{is}~~is~~ insufficient to allow a choice between sympatric and allopatric theories of speciation. The implications of the allopatric model for the interpretation of the fossil record of metazoan organisms are discussed in detail here simply because it is the allopatric theory, rather than the sympatric theory, that is preferred by neontologists. The allopatric theory, then, will be compared and contrasted with the picture of phyletic gradualism in the following discussion.

The central concept of the allopatric theory is that new species can only arise in those situations where a small local population on the margin of the overall geographic distribution of the parent species, becomes isolated genetically from the parent population(s). Such local populations are termed "peripheral isolates." If a peripheral isolate is able to survive after cessation of gene flow with the parent population(s), a new species may arise provided that isolating mechanisms are evolved which would prevent re-initiation of gene flow should the geographic distributions of the two groups of populations overlap at

some time in the future. A direct consequence of the allopatric theory, then, is that new fossil species will not be found to "originate" from the postulated parent^{or}_l species at the same time and place in which the ancestral species is found to occur. That is to say, it is theoretically impossible to trace the gradual splitting of a lineage merely by following a certain species up through the local rock column.

Another important consequence of the general theory of allopatric processes is that, since selection always maintains an equilibrium between a population and its local environment, such morphological differences as may be seen between the ancestral species and its descendant are present from close after, if not actually prior to, the onset of genetic isolation. These differences are commonly accentuated when and if the two species become sympatric at a later date. In any event, most of the morphological divergence that takes place in a descendant species occurs early in the differentiation of that species, when the population is small and still adjusting more precisely to local edaphic conditions. After it is fully established, a descendant species is as unlikely to show gradual progressive change as is (or was) the parental species. The consequence for the interpretation of the fossil record is that we should not expect to find gradual morphological divergence between two species which are hypothesized to have an ancestral descendant relationship. Most evolutionary events, in a morphological sense, at the species level are generally thought to occur in a short period of time relative to the total duration of the species. It can be further retrodicted, then, that in terms of the morphological features which enable the taxonomist to recognize two closely related fossil species, there will be little evolutionary change of these inter-specific differentia except at those times where there is good reason to believe that the two species became sympatric for the first time.

This simple series of retrodicted consequences of the allopatric theory can be combined to form an expected pattern potentially seen in the fossil record. Using stratigraphic, radiometric, or biostratigraphic (other than the organisms being studied) criteria, a regional framework of correlation must first be established. Starting with this correlation scheme, patterns of geographic, not stratigraphic, variation among population samples of fossils can be expected to appear. Tracing the fossil species through any given local rock column, so long as no drastic changes in the physical environment are evident, should produce no pattern of constant change, but rather one of oscillations in mean values of morphological variables. New, closely related and perhaps descendant species observed to enter into the rock column should appear suddenly, and show no intergradation with the "ancestral" species as far as the inter-specific differentia are concerned. There should be no gradual increase of morphological differentiation between the two species should both be found to persist for some time in higher stratigraphic levels. Quite the contrary,-- it is possible that the two species would show the greatest amount of differences at the time when the descendant species first appears. Finally, in exceptional circumstances, it may be possible to identify that general area of the known geographic distribution of the ancestral species where the new species most likely arose.

One further, general conclusion is that time and geography are not exactly comparable factors in evolution as has been maintained by some authors (e.g. Sylvester-Bradley, 1951). A direct consequence of the application of the allopatric theory to the fossil record is that most interpopulational differences are to be expected in samples drawn from different geographic areas rather than different stratigraphic levels within the local rock column. The difference is one of adjustment to

a heterogeneous series of micro-environments vs. a general patterns of stasis through time.

The other picture commonly brought to bear on species-level evolutionary problems in the fossil record is that of phyletic gradualism. In this case, the paleontologist is not confronted with a self-contained mechanistic theory from the neontologist. The postulated mechanism for such gradual, uni-directional change is "orthoselection," usually conceived of as a constant adjustment to a uni-directional change in one or more features of the physical environment. The concept of orthoselection represents an attempt to remove the explanation of gradual morphological change from the realms of metaphysics (e.g. "orthogenesis"), and is discussed more fully in a later section. Here it is simply noted that it does not emanate from Drosophila laboratories, but rather represents a hypothetical extrapolation of selection mechanisms observed by geneticists.

The picture of phyletic gradualism has been a dominant theme in evolutionary thought from the earliest days of the acceptance of evolution as a serious scientific concept. Originally formulated as an alternative to the catastrophist view of extinctions and multiple creations, gradualism later emerged triumphant in the debate between the early "mutationists" (e.g. DeVries), who argued for discrete, sudden, and major changes in morphology as the important mechanism of the emergence of evolutionary novelties, and the "selectionists," who maintained that morphological change in evolution is under control of natural selection. As a side effect of the subsequent reconciliation of the two views, where mutations were viewed as the ultimate source of variation, and selection as the guiding, creative element in evolutionary change, the notion of phyletic gradualism finally became entrenched in evolutionary thought.

One effect of the incorporation of the notion of gradualism into evolutionary theory was the eventual abandonment, by most paleontologists, of the idea of adaptive evolution.

of the notion of saltative evolution. In this picture of evolution, species were considered morphologically static entities which remained unchanged throughout their entire span on earth. At intervals, such species could give rise suddenly to new, similarly discrete "species." This view seemed to agree with the "mutation" school of evolutionists, but has been abandoned, for the most part, in the absence of any intelligible mechanism for such a process.

Extrapolation of gradual morphological change under a selection regime to a complete model for the origin of new species fails to recognize the fact that speciation is primarily an ecological (including geographic) process. Natural selection in the allopatric model is involved with adaptation to local edaphic conditions and to the elaboration of isolating mechanisms. Genetic isolation is at least as important as natural selection in allopatric speciation. Phyletic gradualism is in itself an insufficient model to explain the origin of diversity in the present, or any past, biota.

Yet phyletic gradualism remains the prevailing model of the origin of new species in paleontology. At one and the same time, this picture is claimed to be supported by paleontological data and forms the basic theoretical preconception underlying the interpretation of the fossil record. [There is a very widespread, but misguided, belief that paleontologists can "read" phylogeny directly from the rocks; this notion is a direct consequence of the preconception of phyletic gradualism. Perhaps the most elegant statement of this belief was penned by the late W.D. Matthew (1926, p. 454), admittedly in a popular journal:

"Stratigraphic studies and exact records of geological level were developed in the nineties, and added a new and fascinating interest to the work, as one could actually trace in the succession of strata the progressive evolution of the different races, verifying in specimen after specimen the primitive characters of those from the lower layers, the progressive character of those from the upper layers, and the intermediate conditions

in specimens from the middle beds. No one carries a more solid conviction of the truth of evolution than the field paleontologist. He has seen it with his own eyes, and it is quite useless for learned pundits of the pulpit or the laboratory to tell him that evolution is only a hypothesis, or that palaeontology does not prove anything about it. He knows better; he has seen it himself ineffaceably inscribed in the records of the past."

No one would doubt that the fossil record is a mirror, however tarnished, of evolutionary events. But one may seriously question whether evolutionary patterns are as simple as the model of phyletic gradualism would imply.

Even though phyletic gradualism underlies most paleontological discussions of the origin of new taxa, there are relatively few "classic" examples which purport to document this phenomenon. A few authors (e.g. MacGillavry, 1968; Eldredge, In press) have claimed that the relative paucity of such examples simply means that in situ, gradual, progressive evolutionary change is a rare phenomenon. The usual means of explaining the lack of more cases is the by now 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, should the general image of phyletic gradualism be the rule for the evolution of fossil species, then, no matter how discontinuous the occurrence of a species, if it is present near the bottom, occurs sporadically throughout, and is present near the top of a thick sequence, there should be a shift in one or more morphological variables from sample to sample up through the section. This is, in fact, the actual situation in most cases claimed to show gradualism, i.e. the "gradualism" is actually represented by dashed lines connecting known samples. Such a procedure constitutes an excellent case of citing a preconceived model as an "objectively documented" example. One of the early "classic" examples of phyletic gradualism -- Carruthers' (1910)

study of the Carboniferous rugose coral Zaphrentites delanouei (Milne-Edwards and Haime) , as well as its reinterpretation by Sylvester-Bradley (1951) -- is of this kind. This is not to say that the analysis is incorrect; the Zaphrentites delanouei stock may in fact have evolved much as Carruthers and Sylvester-Bradley have claimed. It is merely our intention to place this and other claimed documented examples of phyletic gradualism in their proper perspective.

How pervasive, then, is gradualism in these quasi-continuous samples? A number of authors (including, inter alia, Kurtén, 1965, MacGillavry, 1968, and Eldredge, In press) have claimed that, from the horizon of earliest appearance, most species show little or no change throughout the remainder of their stratigraphic occurrence. But tempting as it may be to conclude that gradual, progressive morphological change is an illusion, it must be recognized that, in actuality, there is little hard evidence to support either view.

Perhaps the most widely familiar example of a sequence commonly interpreted in terms of phyletic gradualism is the fossil record of the family Hominidae. Though many discussions of hominid evolution in the past decade have admitted, or openly championed, the possibility of divergence within the known stratigraphic range of the hominids, Brace (1967 and elsewhere) has recently restated the view that the fossil record of the Hominidae can be interpreted in terms of some four successive "stages" involving direct ancestral-descendant relationships. These are the Australopithecine Stage (with two successive "phases" -- the australopithecus phase, followed by the paranthropus phase), the Pithecanthropus Stage, the Neanderthaloid Stage, and, finally, the Modern Stage. Again, it is not our intent to present a new interpretation of hominid phylogeny, nor to identify any particular one of the several available interpretations as the "best." In his discussion of the history of paleoanthropology, Brace has convincingly shown that

most claims that the hominid fossil sequence does not exhibit ancestral-descendant relationships stem from a desire to avoid the conclusion that Homo sapiens L. 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 known fossils, and the invocation of successive extinctions and subsequent waves of migration of new populations which arose by successive creations. Such views are, of course, absurd. But Brace would include all cladistic interpretations of the hominid fossil record as examples of "hominid catastrophism," and claims that viewing hominid phylogeny as a gradual, progressive, unilineal process involving a series of stages is the interpretation most consonant with modern evolutionary theory. His interpretation of phylogeny may be correct, but he is seriously in error to claim that the preconception of phyletic gradualism is the picture most consistent with modern evolutionary theory. The stage of hominid evolution recognized by Brace and many others may actually be samples of a continuous sequence which we have been fortunate enough to observe. But in view of scanty material, the stratigraphic ranges of these stages cannot be known with any certainty. Quite apart from the issue of possible overlapping ranges of the stages, it would be of the highest interest to determine the degree of stability, i.e. stasis, attained by these stages through any reasonably long period of time. Until the problem is examined more thoroughly from this point of view, the course of hominid phylogeny cannot be considered a settled matter, and the interpretation propounded by Brace and other workers in the past must be recognized as being founded upon the preconceived notion of phyletic gradualism.

At this point, there seems to be some justification for con-

cluding that, on the one hand, the picture of phyletic gradualism is poorly documented indeed, and that most analyses purporting to illustrate this phenomenon directly from the fossil record are largely interpretations based on a preconceived idea. On the other hand, the assertion that 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 largely informal data. The ~~idea~~ of punctuated equilibria is just as much a preconceived "picture," or "model," as that of phyletic gradualism. We readily admit our bias toward the former picture, and in the ensuing discussion of specific examples it must be remembered that our interpretations may be as equally colored by our own preconceptions as we have claimed have been the interpretations of the champions of phyletic gradualism.

The two examples which we present below and which we believe are best interpreted from the point of view of allopatric speciation are drawn from our own work. Hallam (1962) on Gryphaea and Nichols (1959) on Micraster, have fleetingly suggested reinterpretations of two of the classic cases of phyletic gradualism. Other authors have recently presented original studies using the allopatric model as the source of explanation for their evolutionary events. 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 recently presented a detailed analysis of cladogenesis in the pulmonate gastropod Poecilozonites bermudensis zonatus Verrill from the last 300,000 years of the Pleistocene of Bermuda. Specimens were collected from a variable sequence of eolianites and red soils and were most abundant in unindurated zones of the eolianites. Formational names and dominant lithologies are given in Table X.

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

Two distinct types 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 unequivocal cases of introgression. Apparently P. bermudensis zonatus was divided into two parallel evolving stocks, with little or no genetic flow between them, throughout the entire interval of Shore Hills through Southampton time. Both the eastern and western P. b. zonatus became extinct sometime after Southampton time, to be replaced by P. b. bermudensis, an apparent derivative of eastern P. b. zonatus which had been evolving separately on St. George's Island since St. George's time. Gould (1969, 1970) has discussed the parallel oscillation of various morphological variables in both stocks of P. b. zonatus, interpreted as adaptive shifts to glacially controlled climatic variations. Both stocks exhibit stability in other features which serve to distinguish them from their nearest relatives. In no case does there appear any evidence for gradual divergence between eastern and western P. b. zonatus.

A number of samples of P. bermudensis share some ten attributes in common by which they may be distinguished from P. bermudensis zonatus. These ten characters can be thought of in terms of four categories: color, general spire form, nature of the callus, and shape of the outer apertural lip. The ontogeny of P. b. zonatus indicates that these four categories are closely interrelated. Immature shells of P. b. zonatus are weakly colored, lack a callus, are relatively wide, and have the lowest portion of the outer apertural lip at the umbilical border. This combination of character states is exactly repeated in

mature specimens of the non-zonatus samples of P. bermudensis.

Since every characteristic ontogenetic feature developed at or after the fifth whorl in these samples is attained by whorls 3-4 in P. b. zonatus, Gould (1969) concludes that the non-zonatus samples of P. bermudensis are paedomorphically derived from P. b. zonatus.

These paedomorphic samples are known from the entire interval from Shore Hills to the Recent. The most obvious hypothesis would be that they constitute a continuous lineage evolving separately from P. b. zonatus. ^{We?} Gould rejects this hypothesis and concludes that paedomorphic offshoots were derived from the P. b. zonatus stock four different times, basing his arguments on details of stratigraphic and geographic distribution as well as morphology.

Fig. A summarizes the history of phylogenetic splitting of the P. b. zonatus lineage
The earliest paedomorph known, 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 a 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 other known post-Shore Hills P. bermudensis.

In the succeeding Harrington Formation, paedomorphic samples of P. bermudensis are known from both the eastern and the western geographic zones 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 and the contemporaneous population of eastern P. b. zonatus lack the distinctive features of all Shore Hills P. bermudensis and the more economical hypothesis is that the unique set of features which unite 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 P. b. zonatus. Very simply, P. b. sieglindae is found in eastern Bermuda and shares the color banding pattern of eastern P. b. zonatus, while P. b. siegmundi is found in western Bermuda and possesses the same color pattern as western P. b. zonatus. In addition, both P. b. sieglindae and P. b. siegmundi evolved, judging from the known geographic distributions of these subspecies, on the periphery of the range of their putative ancestors. The independent derivations of the two Harrington paedomorphs from the two separate stocks of P. b. zonatus seem clear.

Finally, the extant ^{paedomorph} P. bermudensis bermudensis first appears in the St. George's Formation on St. George's Island. While St. George's Island is also within the geographic range of eastern P. b. zonatus, it is far removed from the presumed area of origination of P. b. sieglindae. Gould concludes that P. b. sieglindae was a short-lived population that never enjoyed a wide distribution; he estimates that the distribution of the Pembroke population probably did not exceed 200 yards. While there is no formal, compelling morphological argument, then, Gould recognizes a fourth paedomorphic subspecies, P. b. bermudensis, derived directly from (eastern) P. b. zonatus. The conclusion is totally consistent with, and in fact based on, geographic and stratigraphic data.

Gould (1969) has advanced an explanation in adaptive terms of the four separate origins of the paedomorphic populations from P. b. zonatus. This explanation need not be recapitulated here. What is important for present purposes is to emphasize that the reconstruction of the phylogenetic histories of the paedomorphs was based on (1) attention to geographic data (the allopatric model), (2) discontinuous strati-

graphic occurrences (a more literal interpretation of the fossil record), and (3) formal arguments based on morphology. It is entirely possible to interpret the three paedomorphs of the eastern P. b. zonatus area as a gradational biostratigraphic series.

Fig. B shows a temptingly possible interpretation of phyletic gradualism of "lower eccentricity," an apertural variable. Values gradually increase through time. Fig. C, however, confounds such an interpretation by indicating that the stratigraphic variability in the "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, which might be taken to indicate that each subspecies is unique and that they are not necessarily closely related.. In fact, neither graph affords sufficient evidence to warrant either conclusion. Morphology, stratigraphy, and geography must all be evaluated when the history of a closely related group of taxa is being analyzed.

Another example which demonstrates the retrodicted patterns of the allopatric process is the phylogenetic history of the trilobite Phacops rana (Green) from the Middle Devonian of North America (Eldredge, 1969 and In press). As in the case of Poecilozonites bermudensis zonatus, full genetic isolation is thought not to have been established between "parent" and "daughter" taxa; such a conclusion is based on inferences of degree and kind of morphological variability, and may be wholly unwarranted. For the present purposes, it is irrelevant whether we are dealing with four subspecies of P. rana, or four separate species of Phacops, including P. rana and its three closest relatives. Clearly the basic evolutionary mode underlying the phylogenetic history of the group as a whole is the same in either case.

Certain features of eye morphology exhibit the greatest amount of variation among population 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 of any population is reached quite early in ontogeny. The number of dorso-ventral (d.-v.) files is the most important feature to display interpopulational variation in P. rana.

The closest known relative of P. rana is P. schlotheimi^(Bronn)/S.I., from the Eifelian of Europe and Africa; this group has recently been revised by C.J. Burton (1969). In addition, several samples referable to P. rana are known from the Spanish Sahara in northwestern Africa (Burton and Eldredge, Ms.). P. schlotheimi and the African specimens of P. rana are most closely similar to P. rana milleri Stewart and P. rana crassituberculata Stumm, the two oldest subspecies of P. rana known in North America. All of these taxa possess eighteen dorso-ventral files; without further argument here (but see Eldredge, 1969), we conclude that eighteen is the primitive number of d.-v. files for all North American Phacops rana.

Fig. D summarizes the relationships of the four subspecies of P. rana, without regard for stratigraphic occurrences. The oldest examples of P. rana known in North America occur in the Lower Cazenovian Stage of Ohio and central New York State. All have eighteen d.-v. files. Populations with eighteen d.-v. files persist into the Upper Cazenovian Stage in the epicontinental seas generally west of the marginal basin of New York and the Appalachians to the south. P. rana milleri and P. rana crassituberculata, both of which possess eighteen d.-v. files, are distinguished on criteria other than those discussed here; although their interrelationship is itself interpretable in geographic terms, it will not be mentioned further.

One of the two populations known to show intra-populational variation in d.-v. file number occurs in the Lower Cazenovian of central New York. Some specimens display eighteen d.-v. files, while

others show the first d.-v. file in various states of reduction; a few lack the first d.-v. file altogether. All P. rana known from subsequent, younger horizons in New York and adjacent Appalachian states have seventeen dorso-ventral files. Apparently, then, seventeen d.-v. file P. rana rana arose from an eighteen d.-v. file P. rana population on the northeastern periphery of the known Cazenovian geographic range of P. rana. Seventeen d.-v. file P. rana persist, unchanged in most respects, throughout 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 eighteen d.-v. file populations which apparently became extinct during a general withdrawal of marine conditions from the continental interior. All known Tioughniogan P. rana, then, possess seventeen dorso-ventral files.

A second, similar event involving reduction in the number of dorso-ventral files is seen in the Taghanic. Here again, a variable population is known in New York, suggesting that somewhere in this general area on the periphery of the known range of P. rana rana, reduction in d.-v. file number was accomplished allopatrically. The spread of the stabilized, fifteen d.-v. file eye variant P. rana norwoodensis through the Taghanic seas of the continental interior was instantaneous in terms of our biostratigraphic resolution. Fig. F summarizes this interpretation of the history of P. rana.

Though the entire history of the P. rana stock is more complex than the brief version presented here, the basic pattern of the emergence of discrete sub-taxa is apparent. The picture is one of stasis, i.e. no variation in the single most important interpopulational variable (number of d.-v. files -- actually a complex of highly interrelated variables) through long spans of time. Relatively "sudden" events of reduction in the number of dorso-ventral files on the periphery of the

(known) range are pinpointed by the existence of the only two documented population samples displaying intra-populational variation in d.-v. file number. These two population samples, moreover, have a very short stratigraphic, as well as a restricted geographic, distribution. Patterns of distribution, important to the biostratigrapher, are intelligible only from a perspective incorporating notions of competitive exclusion, extinction, and migration.

We thus propose that the allopatric model can be effective in explaining the results of the evolutionary process as seen in the fossil record. This suggestion is by known means original, yet it may still be fairly stated that the picture of phyletic gradualism, buttressed by the concept that phylogeny can be read directly from the rocks, is the predominant theme underlying most paleontologists' expectations upon initiating an investigation of a suite of closely related fossil species. Our alternative picture is merely the application, in gross outline, of the dominant theory of speciation in modern evolutionary thought to the fossil record. We firmly believe that the retrodicted consequences of this model are more nearly in accord with the fossil record of the vast majority of the fossil Metazoa.

(SOME COMMENTS ON TRENDS)

Trends, or biostratigraphic character gradients, are frequently mentioned in conjunction with the fossil record of many groups of organisms. A trend is generally taken to mean a consistent change in one or more morphological features and has commonly, but not always, been discussed in terms of phyletic gradualism. Sequences of fossils alledgedly displaying trends range from the infra-specific through the very highest categories within the taxonomic heirarchy. Trends at the species and infra-specific level always amount to phyletic gradualism and have been discussed above. The relation between the notion of phyletic gradualism and trends involving larger, phylogenetically related clusters of species -- e.g. a family or an order -- remains to be examined.

The very real possibility exists that many, if not most, of the trends involving higher taxa may be based on a selective rendering of elements of the fossil record which are chosen because they seem to form a morphologically graded series coincident with a progressive biostratigraphic distribution. Whether considered to be the result of the general family of metaphysical processes we may lump together, somewhat uncritically, as "orthogenesis," or the result of the perhaps more scientific, but intrinsically untestable process of "orthoselection," many trends may in fact represent simple extrapolations of the picture of phyletic gradualism.

It would seem, however, that maintaining that all documented trends are merely unwarranted extrapolations based on a preconception constitutes altogether too facile an explanation for the large number of examples of trends cited in the literature. For the purposes of this discussion, we will accept the existence of trends as a real and important phenomenon in evolution, and adopt the simple defintion given by MacGillavry (1968, p. 72): "A trend is a direction which involves the majority (*italics ours*) of related lineages of a group."

If trends are real, common phenomena, how can they be reconciled with a picture of speciation events as punctuated equilibria, where such adaptation as occurs in the peripheral isolates is largely involved with local edaphic conditions and the perfection of isolating mechanisms? The problem may be stated in another way: Sewall Wright (1967, p. 120) has pointed out that, just as mutations are stochastic with respect to selection within a population, so might one postulate that speciation is stochastic with respect to the origin of higher taxa. A slight extension of that statement would be that adaptation to local edaphic conditions by peripheral isolates ^{is} are stochastic with respect to long term, net directional change (i.e. trends) within a higher taxon as a whole. We are left with a bit of a paradox, since to picture speciation as an allopatric phenomenon involving rapid differentiation within a general, long-term picture of stasis, is to deny the model of directed gradualism in speciation. But "punctuated equilibria" are in a way more difficult to reconcile with apparently valid cases of long-term trends involving many species.

The quandary is, in a very real sense, incapable of solution, since the mechanisms of any processural theory must come from observations of living organisms. We are in a gray area where we seek to extrapolate mechanisms known to be operative in short-term processes and to apply them to events of very long duration in the fossil record.

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

A reconciliation of allopatric speciation and long-term trends, then, might be developed along the following lines. We might envision multiple "explorations," or "experimentation^s," which are invasions,

on a stochastic basis, of new environments by peripheral isolates. There is nothing inherently directional about these invasions. However, a certain definable subset of these new environments may consistently, in the context of the inherited genetic constitution of the ancestral components of the lineage, lead to new and improved efficiency. Such improvement in efficiency would be consistently greater within this hypothetical subset of edaphic conditions which a population may invade. The overall effect may then be one of net, apparently directional change, but, as in the case of selection acting on mutations, the initial variations are stochastic with respect to this change. This is not to postulate a new type of selection. Rather, it is simply a view of long-term, superficially "directed" phenomena which is more in accord with current allopatric speciation theory, and which avoids the essentially non-testable concept of "orthoselection."

References Cited

- Brace, C. Loring, 1967, The Stages of Human Evolution, 116 pp.,
Prentice-Hall, Inc., Englewood Cliffs, New Jersey. (Steve--
this book is an ^{un}numbered part of the "Foundations of Modern
Anthropology Series edited by Marshall Sahlins and maybe should
be referenced as such.)
- Burton, Christopher J., 1969, Variation studies of some phacopid
trilobites of Eurasia and North West Africa, Ph. D. Thesis,
University of Exeter, England, 222 pp.
- Carruthers, R.G., 1910, On the evolution of Zaphrentis delanouei in
Lower Carboniferous times, Quarterly Journal of the Geological
Society, vol. 66, pp. 523-538.
- Clarkson, E.N.K., 1966, Schizochroal eyes and vision of some Silurian
acastid trilobites, Palaeontology, vol. 9, pp. 1-29.
- Eldredge, Niles, 1969, Geographic variation and evolution in Phacops
rana (Green, 1832) and Phacops iowensis Delo, 1935, in the
Middle Devonian of North America, Ph. D. thesis, Columbia
University, New York, 296 pp.
- Eldredge, Niles, In press, The Allopatric model and phylogeny in Paleo-
zoic invertebrates, Evolution.
- Gould, Stephen J., 1969, An evolutionary microcosm: Pleistocene and
Recent history of the land snail P. (Poecilozonites) in
Bermuda, Bulletin of the Museum of Comparative Zoology, vol. 138,
no. 7, pp. 407-532.
- Gould, Stephen J., 1970, Coincidence of climatic and faunal fluctuations
in Pleistocene Bermuda, Science, vol. 168, pp. 572-573.
- Hallam, A., 1962, The evolution of Gryphaea, Geological Magazine, vol.
99, no. 6, pp. 571-575.

Kurtén, B., 1965, Evolution in geological time, In Moore, J. A.,
(ed.), Ideas in Modern Biology, Natural History Press,
New York, pp. 329-354.

MacGillavry, H.J., ¹⁹⁶⁸ Modes of evolution mainly among marine invertebrates,
Bijdragen tot de dierkunde, vol. 38, pp. 69-74.

Matthew, W.D., 1926, Early days of fossil hunting in the high plains,
Natural History, vol. 26, no. 5, pp. 449-454.

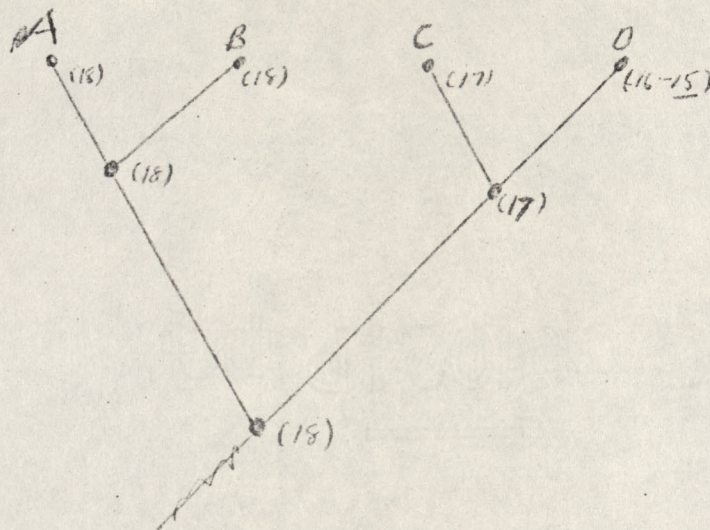
Nichols, D., 1959, Changes in the chalk heart-urchin Micraster
interpreted in relation to living forms, Philosophical
Transactions of the Royal Society of London, B., vol. 242,
pp. 347-437.

Wright, S., 1967, Comments on the preliminary working papers of Eden
and Waddington, in Moorehead, P.S., and M.M. Kaplan, (eds.),
Mathematical challenges to the neo-darwinian interpretation
of evolution, The Wistar Institute Symposium Monograph no. 5,
The Wistar Institute Press, Philadelphia, pp. 117-120.

Sylvester-Bradley, P.C., 1951, The subspecies in paleontology,
Geological Magazine, vol. 88, pp. 88-102.

Steve: I am omitting a reference in the text to "Burton and Eldredge,
Ms." because we have no title for it as yet. O.K.?

Fig. D (Finished version to follow)



Outline of relationships of four subspecies of Phacops rana.

A -- Phacops rana crassituberculata Stumm ; B -- P. rana milleri Stewart;
 C -- P. rana rana (Green); D -- P. rana norwoodensis Stumm. Numbers
 in parentheses refer to number of dorso-ventral files typical of
 subspecies or hypothesized to characterize ~~primit~~ condition of
 common ancestor

E Hypothesized

xin

Figure 5. 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 ~~exogeo-~~ *marginal* ~~com-~~ *crosses denote* ~~syncline~~ *sea* other than that in which the derived taxon occurs. ~~com-~~ *disappearance* *final* ~~pare figure 2D;~~ for fuller explanation, see text.

Fig. 5 *E*

