

# Reports

## Origin of Species in Geologic Time: Alternatives to the Eldredge-Gould Model

**Abstract.** *Formal statements of the Eldredge-Gould model, which proposes that new species have originated almost wholly through evolution in small peripheral isolate populations, and the phyletic gradualism model, which proposes that new species have originated through phyletic evolution in large, widely distributed populations, clarify the relationship of these models as extremes in a spectrum of possibilities, and suggest alternative models incorporating elements of both.*

Eldredge and Gould (1) recently advanced the hypothesis that new species have arisen, in almost all cases, by speciation (splitting of lineages) through rapid evolution in small peripheral isolate populations (2). [I have added the qualifying phrase "in almost all cases"; it does not appear in the explicit statement of their hypothesis (1, p. 96), but it is clear from subsequent discussions that they do not rule out the possibility of occasional, albeit rare, origins through phyletic evolution in ancestor-descendant populations of established species.] Rapid evolution in small peripheral isolates is widely held by biologists to be the principal means of speciation (3), as Eldredge and Gould admit, and it has been utilized in interpretations of fossil populations in earlier works (4). Still, Eldredge and Gould deserve credit for introducing the hypothesis to the overwhelming majority of English-speaking paleontologists and calling attention to its paleontologic implications.

Eldredge and Gould contrasted their hypothesis with an alternative that they termed phyletic gradualism (1, p. 89), which is contrary but not contradictory to it (so that while both hypotheses cannot be true, both can be false). Phyletic gradualism postulates that new species have arisen through slow evolution in ancestor-descendant sequences of populations (phyletic evolution); this involves large numbers, usually the entire population, over all, or a large part, of the ancestral species range. Speciation is allowed (1, p. 94), although the statement that the evolutionary change usually involves the entire population implies that it is rare; speciation in small peripheral isolate populations is ruled out. I doubt that this hypothesis is as widely held as Eldredge and Gould envisage; in particular, I think few paleontologists would completely rule out the possibility of rapid speciation in small peripheral isolates.

The relationships of the two hypotheses

to one another and to alternatives are most easily seen if they are stated formally. For any two sets A and B, let  $A \cdot B$  be the set of elements belonging to both A and B,  $A \vee B$  the set of elements belonging to A or B or both, and  $\sim A$  the set of all elements not belonging to A. Further, let  $P(A, B)$  be the probability of B given A, or the relative frequency of occurrence of members of set B within set A, using the notation of Reichenbach (5); S the set of all the species of sexually reproducing Metazoa which have existed in geologic time (6);  $S_i$  the set of all species belonging to S which originated by speciation in small peripheral isolate populations; and  $S \cdot \sim S_i$  the set of all species belonging to S which did not originate by speciation in small peripheral isolate populations. The Eldredge-Gould hypothesis may then be stated

$$P(S, S_i) = 1 - \epsilon$$

where  $\epsilon$  is some very small number (considerably less than 0.1, say). And the hypothesis of phyletic gradualism may be stated

$$P(S, \sim S_i) = 1$$

which is equivalent to

$$P(S, S_i) = 0$$

Stanley states the Eldredge-Gould hypothesis somewhat differently in terms of the amount of change occurring during phyletic evolution compared with that occurring by speciation in small peripheral isolates; that is, the effect of phyletic change "is minor with most change occurring in speciation events" (7, p. 646) and gradual change within established species "is generally slow and of minor consequence relative to changes that frequently occur in speciation events" (7, p. 648). I note that this phrasing of the hypothesis may be similarly stated formally as follows. Let C be the set of all small discrete permanent character changes that have occurred in the evolution of species of sexually reproducing Metazoa (8) and  $C_i$

the set of all such changes which developed through speciation in small peripheral isolate populations. Then the Eldredge-Gould hypothesis is

$$P(C, C_i) = 1 - \epsilon$$

and the hypothesis of phyletic gradualism is

$$P(C, C_i) = 0$$

When stated as above, it is clear that the two hypotheses are end members of a spectrum of possibilities

$$0 \leq P(S, S_i) \leq 1$$

or

$$0 \leq P(C, C_i) \leq 1$$

I suggest instead a more conservative hypothesis or, more precisely, an infinite family of hypotheses of the form

$$a \leq P(S, S_i) \leq b$$

or

$$a \leq P(C, C_i) \leq b$$

where  $a > 0$  and  $b < 1$  (and not negligibly less as above; for example,  $a = 0.5$  and  $b = 0.8$ ).

Eldredge and Gould's principal and compelling point in favor of their hypothesis is that homeostatic mechanisms resist change in large well-established populations. Still, there must be a limit to this stabilization. Consider two large isolates of an initially continuously distributed population on opposite sides of a major barrier (for example, the Atlantic Ocean for tropical forms), both of which remain large and do not split further for say 10 to 20 million years. It is plausible that they would not be able to interbreed if reunited; indeed it seems at least conceivable that such events happened frequently in geologic time. There appear to be well-documented reconstructions that postulate gradually changing ancestor-descendant sequences of very widely distributed species; examples are the evolutionary schemes inferred for species of *Eocoelia* (9, 10) and *Stricklandia* sensu lato (10, 11), brachiopod genera of the Silurian (~430 to 400 million years ago) which include species that are widely distributed over much of the globe.

Stanley (7) proposed several critical tests, involving the fossil record, to evaluate the Eldredge-Gould hypothesis against phyletic gradualism. Yet, even if the latter hypothesis

$$P(S, S_i) = 0 \text{ or } P(C, C_i) = 0$$

does fail his tests, the alternative

$$0 < P(S, S_i) < 1 - \epsilon$$

or

$$0 < P(C, C_i) < 1 - \epsilon$$

does not. His argument is analogous to a defense of laissez-faire capitalism by saying "but surely you don't prefer Maoist communism"; this enthymematic argument is not valid even if laissez-faire capitalism is eminently desirable.

Paleontologists will never be in a position to decide which of these hypotheses is correct, although we may be able to rule out extreme hypotheses such as phyletic gradualism and its counterpart  $P(S, S_i) = 1$  [or  $P(C, C_i) = 1$ ], an extreme version of the Eldredge-Gould hypothesis, by providing counterexamples. The frequency at which we might expect new species to originate by gradual changes in ancestor-descendant sequences of large established populations over geologic time must be determined, if it is determined at all, by population geneticists.

CHARLES W. HARPER, JR.  
School of Geology and Geophysics,  
University of Oklahoma,  
Norman 73069

#### References and Notes

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2. N. Eldredge, *Evolution* 25, 156 (1971).
3. E. Mayr, *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, Mass., 1963), p. 513; L. Brundin, in *Current Problems of Lower Vertebrate Phylogeny*, Tor Ørvig, Ed. (Almqvist & Wiksell, Stockholm, 1968), p. 473; L. Croizat, G. Nelson, D. E. Rosen, *Syst. Zool.* 23, 265 (1974) (see pp. 269, 270 and 279-280).
4. F. Bernard [*Éléments de Paléontologie* (Baillière, Paris, 1895)], L. A. Nevesskaya [*Paleontol. J.* 1 (No. 4), 1 (1967)], and V. N. Ovcharenko [*ibid.* 3 (No. 1), 57 (1969)] cite examples to document the origin of fossil species through speciation in peripheral isolate populations, although Nevesskaya does not regard this as necessarily the main mechanism of speciation. V. Ruzhentsev [*Int. Geol. Rev.* 6, 2204 (1964)] postulates that fossil species originated rapidly (in less than 1000 years) and subsequently changed little, if at all, so that transitional forms should be rare in the fossil record; he did not restrict their origin to small peripheral isolates.
5. H. Reichenbach, *The Theory of Probability* (Univ. of California Press, Berkeley, 1971).
6. For the purpose of this discussion, I assume that (i) all (known and unknown) ancestor-descendant sequences of fossil populations with distinctive end members have been divided into species comparable in scope to modern-day species, in the manner suggested by A. L. McAlester [*J. Paleontol.* 36, 1377 (1962)] and T. R. Waller [*ibid.* 43 (part 5 Suppl.), 8 (1969)], and (ii) all reproductively isolated populations (known and unknown) existing in any given time interval have been divided into separate species.
7. S. M. Stanley, *Proc. Natl. Acad. Sci. U.S.A.* 72, 646 (1975).
8. For the purpose of this discussion, we will assume that all of the changes occurring, including those in continuous variates such as the ratio of orbit size to skull width in vertebrates, have been characterized as occurring in small, discrete steps; this could easily be accomplished for a continuous variate in any particular case by defining class intervals.
9. A. M. Ziegler, *Palaeontology* 9, 542 (1966).
10. W. B. N. Berry and A. J. Boucot, *Geol. Soc. Am. Spec. Pap.* 102 (1970), p. 28.
11. On *Stricklandia* evolution see A. Williams, *Q. J. Geol. Soc. Lond.* 107, 85 (1951); T. W. Amsden, *J. Paleontol.* 40, 1012 (1966); and W. B. N. Berry and A. J. Boucot (10). A recent study of Siluro-Devonian *Gypidula* species [J. H. Makurath and E. J. Anderson, *Evolution* 27, 303 (1973); J. H. Makurath, *ibid.* 28, 481 (1974)] purports to document gradual change in ancestor-descendant lineages, but the available data are limited and, in contrast to those for *Ecocelia* and *Stricklandia*, only local in scope.

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## Paleomagnetic Excursions as Magnetostratigraphic Horizons: A Cautionary Note

**Abstract.** *Sediments from certain environments with high rates of deposition are not remagnetized after they have been deformed. The paleomagnetic signature from a zone of deformation can be misinterpreted as evidence for globally coherent fluctuations in the earth's magnetic field.*

Recent paleomagnetic studies of sediments from environments with high rates of deposition have provided evidence that, at one or more times during the past 50,000 years, the earth's magnetic field may have exhibited large-scale fluctuations in direction. In view of the lack of a standard terminology, I shall use the term "paleomagnetic excursion" to designate this anomalous behavior. Several investigators (1, 2) have proposed that paleomagnetic excursions record synchronous, worldwide geomagnetic phenomena and therefore represent important magnetostratigraphic horizons that could be used as chronological markers in many areas of late Pleistocene research, including sedimentology, archeology, climatology, paleontology, and palynology.

However, despite many studies (3), the nature of the paleomagnetic excursions remains uncertain. In particular, proposed

paleomagnetic excursions do not yet satisfy the requirements of internal consistency within a given sedimentary basin as well as spatial and temporal consistency on a global scale. In this report I will briefly review these inconsistencies and then provide field evidence that demonstrates that at least some anomalous paleomagnetic results may be explained in terms of other processes.

The geomagnetic field is generated by a dynamo within the earth's core. If paleomagnetic excursions represent geomagnetic phenomena, they must arise from instability in the fluid motions of the core. In this case magnetic potential theory requires that paleomagnetic excursions have a coherent variation on a scale of at least several hundred to a thousand kilometers. We expect therefore that evidence for a paleomagnetic excursion should be internally consistent within sedimentary basins the size of lakes or small seas. Most anomalous paleomagnetic directions represent the results of a study of a single piston core from a given sedimentary basin. When multiple cores have been taken, the results have not always been internally consistent. For example, of 15 cores taken from the Gulf of Mexico (4), only eight appeared to record the excursion. More importantly, the magnetic signature, that is, the precise variation of declination and inclination, varied markedly from core to core.

Difficulties are also encountered when paleomagnetic excursions are examined for spatial consistency on a global scale. A set of paleomagnetic anomalies from northern and central Europe, eastern Canada, the Gulf of Mexico, and New Zealand, with dates clustering around 12,500 years before the present (B.P.), has been interpreted as a global geomagnetic fluctuation and has been named the Gothenburg flip (1). However, the event is apparently not recorded in sedimentary sequences of the same age in southern Europe (5), the Mediterranean Sea (6), and western North America (7).

Finally, there is a lack of temporal consistency in the ages of paleomagnetic excursions. In addition to the cluster of dates around 12,500 B.P., other excursions have been reported in the intervals 15,000 to 20,000 years B.P. (8), 24,000 to 25,000 years B.P. (9), 28,000 to 30,000 years B.P. (10), and 38,000 to 40,000 years B.P. (11).

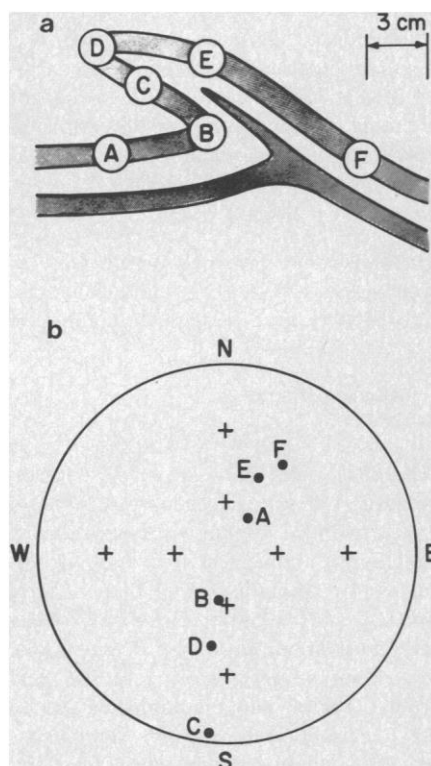


Fig. 1. (a) Vertical cross section showing the location of samples from a fold in varved sediment. The shaded portion represents the winter (clay) layer; the unshaded portion represents the summer (silt) layer. (b) Remanent magnetic directions of samples plotted on a stereographic projection. Samples were demagnetized in a 350-oersted alternating field.