Origin and evolution of species :
evidence from the fossil record

par

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Résumé. Gradualisme phylétique et équilibres ponctués sont deux hypothèses concurrentes concernant le rythme et la modalité de l'évolution au niveau spécifique étudiés à une échelle accessible dans les archives fossiles. Elles peuvent être traitées en comprenant les distributions (calculées) et observées des taux évolutifs et aussi en étudiant en détail des exemples évolutifs concrets caractéristiques. Les taux d'évolution prédits par le modèle du gradualisme phylétique sont distribués suivant le mode gaussien (autour d'une moyenne nulle). Les taux d'évolution prédits par le modèle des équilibres ponctués ont une distribution trimodale, avec un pic étroit à la valeur zéro séparé de 2 modes larges, correspondant aux taux négatif et positif élévés. La distribution de taux évolutifs, telle qu'elle ressort des archives fossiles remises à jour, s'accorde plus avec le modèle du gradualisme phylétique qu'avec celui des équilibres ponctués, mais ceci peut n'être qu'un artefact résultant de l'estimation moyenne du temps.

Les distributions des taux ne constituent cependant pas un test péremptoire pour les deux modèles. L'étude biostratigraphique détaillée des mammifères du début du Cénozoïque dans l'ouest de l'Amérique du Nord tend à corroborer le modèle de gradualisme phylétique. Des « ponctuations » apparentes sont souvent coordonnées dans le temps et elles peuvent être expliquées comme résultant d'une dispersion géographique, en réponse à un changement climatique et à d'autres facteurs extrinsèques. La sélection naturelle suffit à expliquer la forme et la distribution des espèces et il n'est pas besoin d'invoquer l'« homéostasie génétique » comme un mécanisme régulateur plus ou moins mystique.

Abstract. Phyletic gradualism and punctuated equilibria are two competing hypotheses about the tempo and mode of species-level evolution studied on a scale accessible in the fossil record. These hypotheses can be tested by comparing predicted with observed distributions of evolutionary rates, and they can be tested by examining actual evolutionary case histories in detail. Rates of evolution predicted by the phyletic gradualism model are normally distributed about a zero mean. Rates of evolution predicted by the punctuated equilibria model are trimodal, with a narrow peak at zero and separate broad modes at high positive and negative values. The distribution of evolutionary rates documented in the fossil record to date conforms to the phyletic gradualism rather than punctuated equilibrium model, but this could be an artifact of time averaging. Rate distributions do not yet provide a definitive test of the two models. Detailed biostratigraphic sampling of early Cenezoic mammals in western North America tends to support the phyletic gradualism model. Apparent "punctuations" are often coordinated in time, and these can be explained as a result of geographic dispersal in response to climatic change and other extrinsic factors. Natural selection is adequate to explain the form and distribution of species, and one need not appeal to "genetic homeostasis" as a mystical regulatory mechanism.

Introduction

Species are widely considered to be basic units of the evolutionary process. Surprisingly, more than one hundred years after natural selection was proposed as the guiding mechanism of evolution, the mode of origin of species and the tempo of their evolution remain poorly understood. Major advances have been made in understanding genetics, ecology, and other aspects of evolutionary biology, but the long-term evolutionary behavior of species is poorly documented. Intervals of time sufficient for the study of species through their entire history, from origin to extinction (or pseudo-extinction), are only available in the geological record. One reason we know so little about the tempo and mode of species-level evolution is that insufficient attention is accorded geological formations preserving relatively complete stratigraphic sequences of faunal and floral evolution through significant intervals of geological time.

Phyletic gradualism and punctuated equilibria are two competing hypotheses describing the tempo and mode of species-level evolution as studied in the fossil record. Two general tests are available for evaluation of these hypotheses. Phyletic gradualism and punctuated equilibria can be tested by comparing predicted with observed distributions of evolutionary rates, and they can be tested by examining actual evolutionary case histories in detail. In this paper I shall outline a test based on the distribution of evolutionary rates to determine which of the current evolutionary models best describes the geometry of mammalian phylogeny. This will be followed by discussion of actual examples from the fossil record illustrating in detail the phyletic history of several early Cenozoic primate lineages.

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Phyletic gradualism or punctuated equilibria ?

The hypothesis of phyletic gradualism is properly attributed to Charles Darwin, who first published a diagram illustrating this model in the *Origin of Species*. Darwin's diagram, reproduced here in figure 1, shows some species (e.g., A) dividing into two or more lineages that change gradually through time : a^1 giving rise to a^{10} through a series of intermediate steps $a^2 - a^9$, m^1 giving rise to m^{10} through a series of intermediates $m^2 - m^9$, etc. Some species (e.g., B) do not change and shortly become extinct. Other species (e.g., E, F) persist unchanged through the whole interval of study, being represented throughout by a graded series of very similar forms. Thus, in the end, a^{10}, m^{10}, E^{10}, and F^{10} remain, being connected to their progenitors A, E, and F, respectively, by a continuous sequence of intermediates. Morphological continuity is the essential ingredient of Darwinian gradualism. The term gradualism, judging from Darwin's diagram, refers to the graded series of intermediates connecting ancestors and descendents, and it does not necessarily denote a particular rate (the abscissa is unscaled). The only implication about rates is that they are symmetrically distributed, positively and negatively, about a zero mean.

The alternative model, represented in modern form by "punctuated equilibria" is also hypothetical : "The idea of punctuated equilibria is just as much a preconceived picture as that of phyletic gradualism" (Eldredge and Gould, 1972, p. 98). In this model, species are regulated by some unspecified form of "genetic homeo-stasis" that, once set, automatically eliminates variant phenotypes. Evolutionary change occurs in small, peripheral, isolated populations in "alien" environments when selection pressures are able to overcome homeostatic regulatory mechanisms, leading to a "genetic revolution" (Eldredge and Gould, 1972, p. 114). The resulting patterns of phyletic change consist of long periods of stasis ("equilibria") interrupted by short intervals of rapid change ("punctuations"). Darwin's diagram in Figure 1 could be modified to represent this view by making all lines of descent run directly up the page (like B, D, and E), with new lineages appearing at random to replace or parallel these through time.

Evolutionary patterns produced by change according to the Darwinian model should consist of ancestors and descendants connected by a continuous graded series of intermediate forms. In the Eldredge-Gould model, ancestors and descendants are sharply distinct. The distribution of evolutionary rates produced by change according to the Darwinian model should be a broad range of rates symmetrical about a single mode centered at zero. The distribution of evolutionary rates produced by the Eldredge-Gould model should have a narrow range of rates centered at zero (equilibrium rates), with accessory modes at high positive and negative values (punctuation rates). Distributions of evolutionary rates predicted by the two models are shown graphically in Figure 2.

The principal theoretical distinction between the gradual and punctuated models is in the inferred mechanism controlling the process. Lineages evolving according to the Darwinian model are guided by natural selection. Lineages evolving according to the Eldredge-
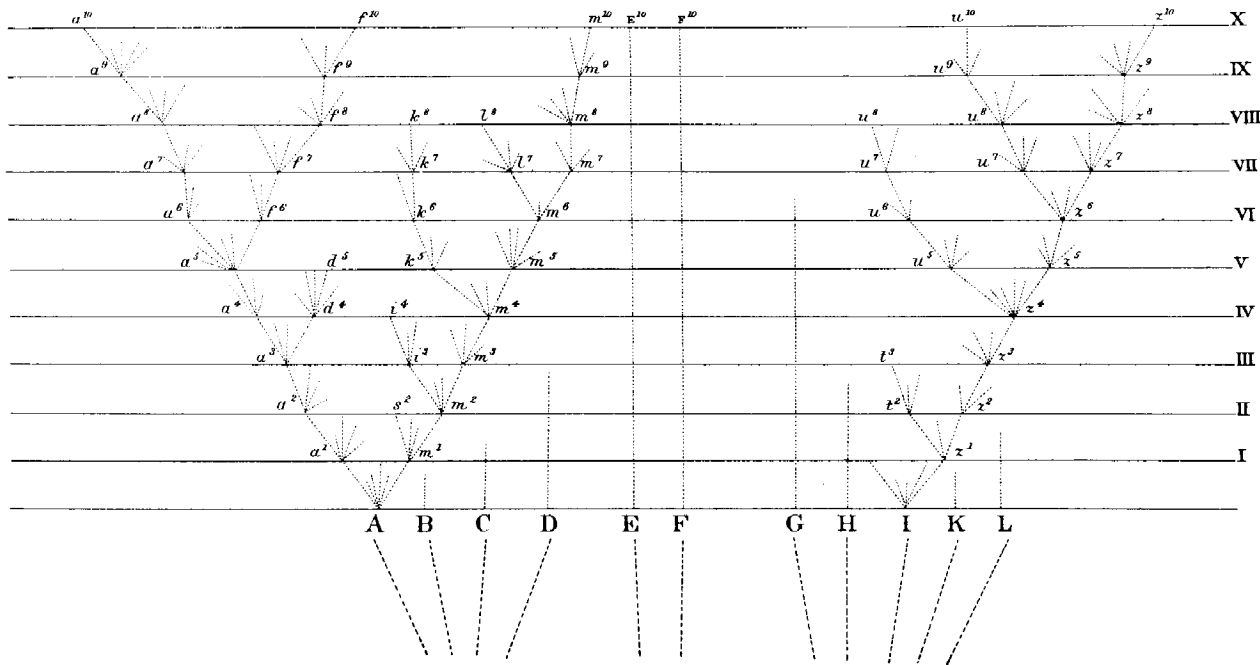

Fig. 1. — Diagram illustrating Darwin's concept of phyletic gradualism. Abscissa unscaled. Horizontal lines with roman numerals (ordinate) represent "a thousand or more generations". Note the origin of species as different as a^{10} and m^{10} by gradual evolution from a common ancestor A, illustrating Darwin's concept of evolutionary divergence of character. Note also that lineages like B, C, D, and E persisted for variable lengths of time without changing. The net effect, including positive and negative rates, might be illustrated by the phyletic gradualism rate distribution show in figure 2. Figure reproduced from the *Origin of Species* (Darwin, 1859).
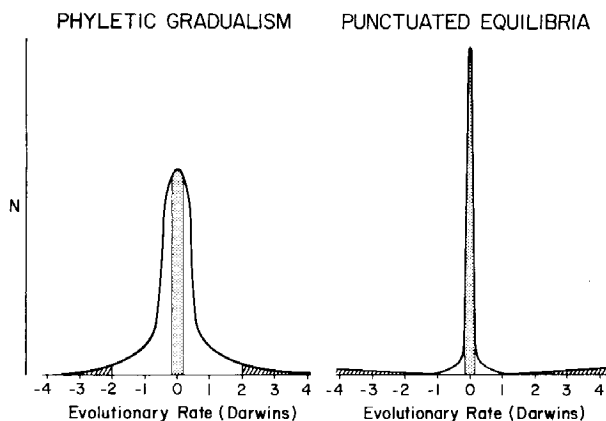
PHYLETIC GRADUALISM   PUNCTUATED EQUILIBRIA

N

-4 -3 -2 -I 0 I 2 3 4   -4 -3 -2 -I 0 I 2 3 4
Evolutionary Rate (Darwins)   Evolutionary Rate (Darwins)

FIG. 2. – Comparison of distributions of evolutionary rates predicted by phyletic gradualism and punctuated equilibria as evolutionary models. Note that in most stratigraphic settings rates greater than about ± 2.0 darwins (crosshatching) could not be detected because the stratigraphic record itself is isufficiently complete (in the sense of Sadler, 1981). Regions of zero mean (stippled areas under curves) do not distinguish the two models because gradual evolution at zero rate cannot be distinguished from static "equilibrium".

Gould model are controlled by some unspecified mystical "homeostatic mechanism" – natural selection in alien environments may have a role to play in overcoming homeostasis during genetic revolutions, but according to the Eldredge-Gould model it has nothing to do with most of evolution.

Distribution of evolutionary rates – a test

Darwin had no means of testing his hypothesis about gradual evolutionary divergence, and worried that imperfection of the geological record might forever preclude such a test. However, the fossil record is much better known today than it was in 1859, and some stratigraphic sections preserve a sufficiently complete and well studied record of faunal history to permit tests of both the phyletic gradualism and punctuated equilibria models. It is clear from the discussion above that these two models differ, in practice, in their predicted distributions of rates of morphological change. Evolutionary rates in phyletic lineages are not yet very fully studied, and no actual rates of change to be expected were specified in framing either model.

Evolutionary change is conveniently measured in *darwins*, where one darwin is understood to be change in a linear measure by a factor of *e* per million years (Haldane, 1949). Change in areas, volumes, and ratios can also be measured in factors of *e* per million years, but these require appropriate scaling for comparison with rates calculated from linear measurements. Counts of linear arrays can be treated as linear measurements for purposes of calculating rates. The principal compilations of evolutionary rates based on the fossil record and calibrated in darwins are by Kurtén (1960), Maglio (1973), and Van Valen (1974). These are biased in three

ways :

1) Zero rates of change are usually ignored because the rates are compiled to see how change itself takes place.

2) High rates of evolutionary change are usually not recorded because stratigraphic completeness is insufficient to preserve any record of them (Sadler, 1981).

3) Measurement of evolutionary rates is strongly dependent on the time interval over which the rate was measured. Short intervals record higher rates, in part, because they are less smoothed (Bookstein, Gingerich, and Kluge, 1978; Gingerich, 1983).

Given these constraints, we might expect that some areas of the distribution of evolutionary rates will be inaccurately represented, as shown in Figure 2. The area of the central zero mean (stippled) and areas more than about two darwins from the mean (crosshatching) are not likely to be represented in most existing compilations of evolutionary rates taken from the fossil record. Nevertheless, one might expect that it should be possible to distinguish between the gradual and punctuated models by the distribution of rates between the stippled and crosshatched portions of the curves.

The gradual model of phyletic evolution predicts a large number of rates between about 0.1 and 2.0 darwins, decreasing from the former to the latter. The punctuated equilibria model predicts a small number of rates between 0.1 and 2.0 darwins, with little or no continuity across this range. Ideally, one would like to know the distribution of evolutionary rates for all taxa in a fauna through a series of successive temporal intervals where the durations of the time intervals themselves were held constant. Data of this quality are not yet available. Kurtén (1960) reports 58 rates for Cenozoic mammals in the 0.003 to 0.2 darwin range, 13 rates in the 0.12 to 2.3 darwin range, and 14 rates in the 3.7 to 4.3 darwin range. All of the 140 rates for Plio-Pleistocene Elephantidae reported by Maglio (1973) are in the 0.0 to 1.0 darwin range, and nearly all of these are between 0.0 and 0.5 darwins. Van Valen (1974) gives 75 rates for invertebrates and protists ranging from 0.0 to 0.3 darwins. Thus the limited data analyzed to date appear to show that the area of the rate/frequency curve between 0.1 and 2.0 darwins includes a large number of evolutionary rates decreasing progressively from 0.1 darwins as predicted by the Darwinian model of phyletic gradualism.

Patterns in the fossil record

The most direct way of testing the phyletic gradualism and punctuated equilibria models is to examine actual patterns of morphological change where these are documented in detail in the stratigraphic record. For the past seven years I have been working with colleagues and graduate students to develop a better understanding of evolutionary change documented in the rich fossil record of early Cenozoic mammals preserved in the Clark's Fork Basin of northwestern Wyoming. Patterns of evolutionary change at a faunal level are reasonably well documented in the Clark's Fork and continguous

Bighorn Basin (Gingerich, 1980; Schankler, 1980; Rose, 1980, 1981). Here I want to discuss two examples that illustrate different aspects of our ongoing research on patterns of evolutionary change at the species level. These examples are discussed at greater length in Gingerich (1980, 1982).

Carpolestidae and Plesiadapidae are two families of archaic primates that are commonly preserved in the middle and late Paleocene of North America (figure 3). Their phylogeny is well documented as a result of monographic treatment by Rose (1975) and Gingerich (1976). Two lineages of carpolestids are known, one represented by *Elphidotarsius* and *Carpodaptes*, and the other by *Carpolestes*. Species of these lineages are characterized by significant differences in dental formulae, dental cusp patterns, and overall size. One lineage of plesiadapid is known initially, represented by *Pronothodectes* and early *Plesiadapis*. This lineage later apparently divided into two. Details of the bifurcation are not yet well known, but this division appears to have taken place during the latter part of the Tiffanian Land-Mammal Age. Subsequently both lineages diverged, with one lineage becoming larger and the other smaller. The transition from *P. fodinatus* to *P. dubius* is not yet well documented, but additional collecting has yielded intermediates between *P. simonsi* and *P. cookei*. Both Carpolestidae and Plesiadapidae appear to have evolved at rates ranging from about 0.0 to 0.5 darwins.

Figure 3 shows that lineages often change significantly through time, with some becoming larger while others become smaller. New lineages may appear abruptly in the fossil record as immigrants from else-

where (*E. florencae, C. jepseni, Pro. jepi*) or they may evolve from lineages already present. Anagenesis and cladogenesis are both important in producing new species.

The early Eocene primate *Cantius* is among the best documented lineages of early primates. Several hundred specimens are known from successive intervals of a 750 meter stratigraphic section representing the first 2 million years of the Wasatchian Land-Mammal Age (ca. 53.5 – 51.5 Ma.). Tooth size of early *Cantius* is plotted by stratigraphic level in Figure 4. A single lineage appears to be present exhibiting considerable variation in evolutionary rates ranging from about – 1.0 to + 1.0 darwins (– 0.5 to + 0.5 darwins for comparison with linear measurements discussed above). This diagram illustrates that short term evolutionary rates may be significantly greater than long term rates. *Cantius ralstoni* first appeared suddenly in the North American fossil record, but this is plausibly attributed to immigration from elsewhere rather than "punctuated" speciation. Subsequent evolution of *Cantius* in the Clark's Fork Basin is documented by many successive samples connecting the first population sample to the last by a graded series of intermediate forms.

Conclusions

Distributions of evolutionary rates and patterns of evolutionary change in relatively complete stratigraphic sections corroborate the Darwinian model of gradual
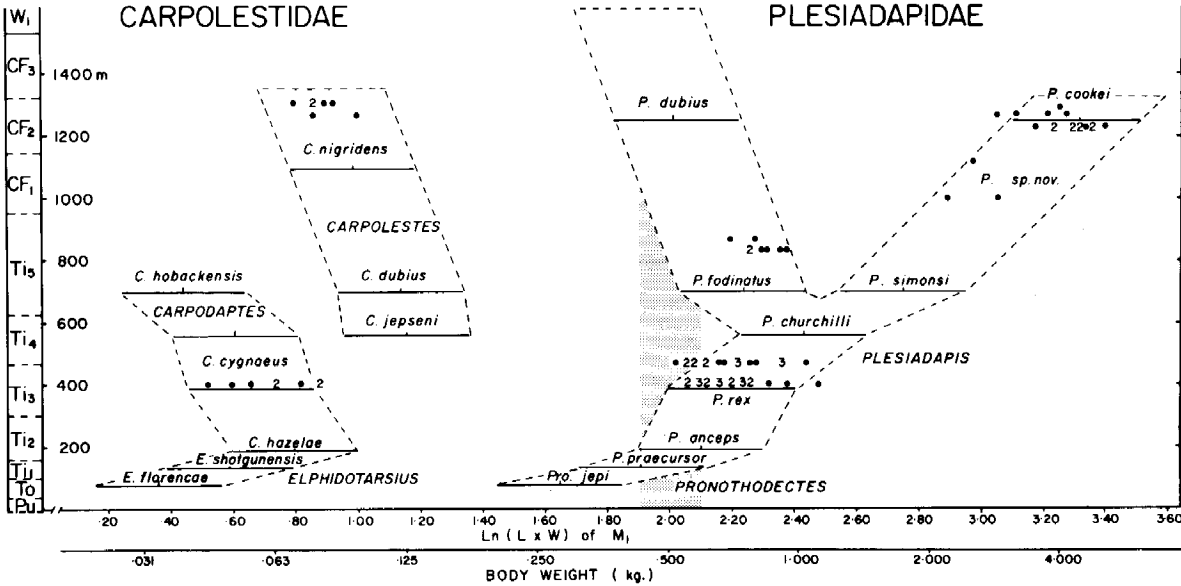

FIG. 3. – Patterns of punctuated and gradual evolution in two families of North American Paleocene primates, Carpolestidae and Plesiadapidae, respectively. The punctuated first appearances of *Elphidotarsius florencae, Carpolestes jepseni*, and *Pronothodectes jepi* are all correlated with episodes of faunal turnover and can plausibly be explained as immigration from some as yet unknown faunal province. Gradual divergence of the *Plesiadapis dubius* and *Plesiadapis cookei* lineages from a *Plesiadapis churchilli* – like ancestor is corroborated by discovery of new specimens intermediate between *P. fodinatus* – *P. dubius* and between *P. simonsi* – *P. cookei*. This cladogenic event is recorded in detail only in the Clark's Fork Basin, Wyoming, but it resumably reflects allopatric speciation in populations covering much larger geographic areas. Figure from Gingerich (1980), based on original data in Rose (1975) and Gingerich (1976).
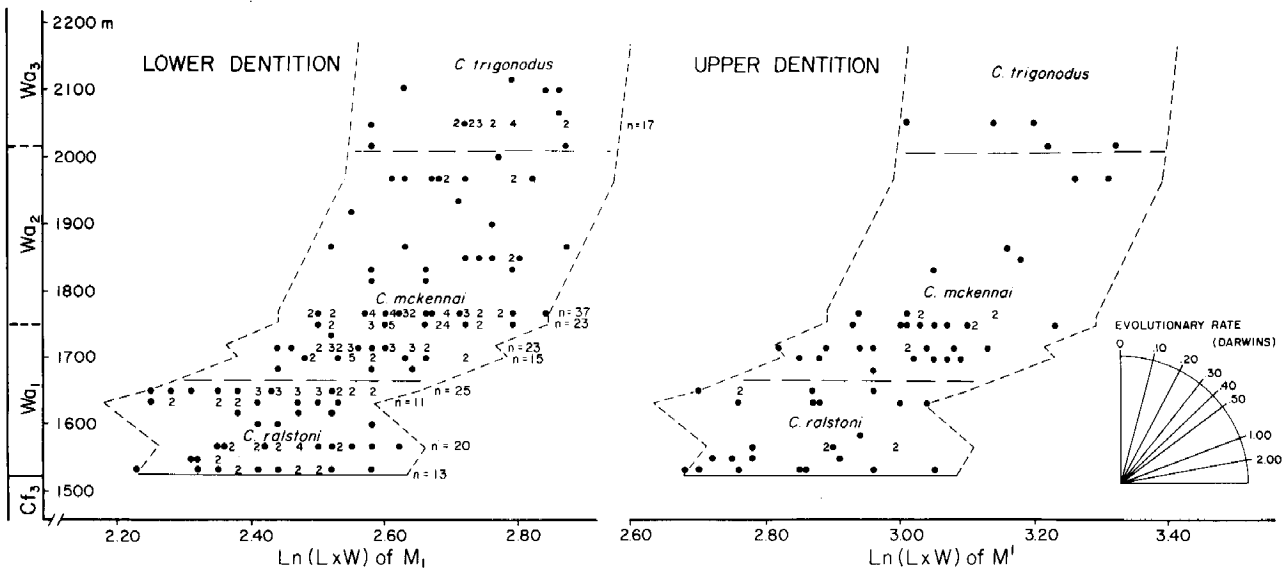
CLARK'S FORK BASIN *CANTIUS*

FIG 4. – Detailed chronocline showing evolutionary change in tooth size in three successive species of one lineage of the early Eocene primate *Cantius*. All specimens are from stratigraphically superposed localities in the Clark's Fork Basin, Wyoming. Note that the maximum rate of increase or decrease in tooth area appears to be about 1.0 darwins at this scale of measurement (0.5 darwins for comparison with change in linear measurements). New species may arise through anagenesis as well as cladogenesis. Figure from Gingerich (1982).

evolutionary change. The same evidence casts considerable doubt on the generality of the Eldredge-Gould "punctuated equilibria" model. Most, if not all, examples of the sudden appearance of new forms in the fossil record *can* be explained by imperfection of the geological record. As Darwin wrote in the *Origin of Species* :

"We continually forget how large the world is, compared with the area over which our geological formations have been carefully examined; we forget that groups of species may elsewhere have long existed and have slowly multiplied before they invaded the ancient archipelagoes of Europe and the United States. We do not make due allowance for the enormous intervals of time, which have probably elapsed between our consecutive formations – longer perhaps in some cases than the time required for the accumulation of each formation. These intervals will have given time for the multiplication of species from some one or some few parent-forms, and in the succeeding formation such species will appear as if suddenly created".

The evolutionary play is staged in an ecological theatre where geography and climate and the evolution of surrounding organisms all have profound effects on the form and dispersion of individual species. In this context, extrinsic rather than intrinsic factors play a dominent role in shaping the history of individual species. Natural selection is an extrinsic mechanism adequate to regulate the form and distribution of species, and nothing in the fossil record requires invocation of a mystical intrinsic "genetic homeostatis" mechanism.

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