

Evolution--a composite model.

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ABSTRACT: The paleontological record, both on land and at sea, is best explained by a composite model of evolution combining three modes--phyletic evolution, extinctive evolution, and the standard model (the updated version of the "modern synthesis" originally proposed by Julian Huxley). Although one mode may be dominant within a given taxon, two or even all three modes may operate concurrently within other taxa, sometimes even within the same lineage. Background extinction, the most common mode of extinction in the long history of life on earth, is attributed to viral (or microbial) action.

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Evolution theory was stabilized in the 1940's by Huxley (1942), Mayr (1942), and Simpson (1944) into a "standard model" involving allopatric (or peripatric) speciation and competitive replacement. These authors (all biologists) viewed evolution essentially as a slow and gradual process, although Simpson (1953) introduced the notion of rapid evolution (which he called *quantum evolution*) in populations moving into different adaptive zones. More recently, Eldredge and Gould (1972) proposed a model, which they called *punctuated equilibrium*, that emphasizes the fact that new species are seen to appear abruptly in the geological record and then to undergo a period of stasis before becoming extinct. According to the authors, this model has now reached adulthood (Gould and Eldredge 1993).

Contrary to the biologists, paleontologists not only have always recognized both the sudden appearance of new species and subsequent stasis (species longevity), but also have been routinely using these events to zone geologic time. Indeed, such ancient terms as *guide fossil* or *index fossil*--a fossil characteristic of a stratigraphic time unit--require sudden appearance followed by stasis for the duration of at least that unit. Lyell (1857) named the Tertiary periods on the basis of the percentage of modern species of marine invertebrates they contained--3.5% for the Eocene, 17% for the Miocene, 35% to 50% for the Older Pliocene, and 90-95% for the Newer Pliocene (renamed Pleistocene by Lyell himself)--which obviously indicated long periods of stasis for these species. By the mid-1950's it had become clear that stasis among marine molluscan species ranged from less than one million years to more than 25 million years (Rensch 1960). (Admittedly, the paleontologist's "species" is not a concept as clear as the biologist's species--at least the biologist's *sexually* reproducing species; paleontologists separate species when the morphologies of the fossils are as distinct as the morphologies of living sister species--that is the best they can do.)

As to the incompleteness of the stratigraphic record to allow for gradual evolution of index species restricted to a single zone, the recognition of 49 graptolite zones from Tremadocian to Ludlovian (a time interval of 100 million years, yielding an average duration of 2.0 m.y. per zone), and of 74 ammonite zones from the Hettangian to the Tithonian (a time interval of 62 m.y., yielding an average duration of 840,000 y per zone) (Harland et al. 1990), with many species restricted to a single zone,

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leaves hardly any time for gradual evolution during the postulated sedimentary hiatuses (see Fig. 42 in Brouwer 1959, for example).

Paleontologists have been reasonably happy with the standard model as accounting for both rapid evolution in peripheral isolates, where environmental conditions are highly variable, and the observed stasis in established species. If they "never wrote papers on the absence of change" (Gould and Eldredge 1993) it is simply because absence of change has been universally self-evident in the fossil record for 200 years. Indeed, it is astonishing to see that, as claimed by Gould and Eldredge (1993), biologists have apparently paid no attention whatsoever to the paleontological literature of the past two centuries. I hope that this lamentable situation will be corrected with the advent of the next century (the CXXIst century; see Emiliani 1994; Roylance 1994).

Stasis, in any case, should not have come as a surprise to the biologists because it is at the very core of evolution theory, for stasis results from a static environment providing the negative feedback that maintains stasis, in many cases across millions of successive generations. A typically static environment is the intertropical open ocean above the thermocline. A planktic foraminiferal mutant whose genes force it to build a shell that is too heavy may sink before it has time to reproduce or, if the shell is too light, it may float to the surface only to be killed by solar radiation or by a squall suddenly freshening the sea water. This is certainly the reason why planktic foraminiferal species occupy specific depths within the narrow range of the photic zone (Emiliani 1954, 1971) and stay there for millions of years. Stability in the biosphere is like stability in a mechanical system--it can be attained only through negative feedback. At the other extreme we have highly variable environments, like marine shelves in the proximity of large freshwater outflows from the continents. Strong seasonal and secular changes occur in salinity and in the quantity and quality of nutrients and other substances from the land. As a result, the populations are stressed and exhibit high variability (see Emiliani 1950 and the foraminiferal populations illustrated by Rögl and Bolli, 1973), and cannot be stabilized except for short periods of time (decades). Indeed, the shelves and bays of the Caribbean and Gulf of Mexico and of the Indonesian seas are probably the best factories of new marine species (and so was the ancient Tethys).

The detailed work of Bolli in Trinidad in the 1950's and 1960's led to a zonation of the entire Tertiary based on planktic Foraminifera (see Stainforth et al. 1975 and Bolli et al. 1985 for historical background). First occurrences and last occurrences demonstrated species longevities ranging, similarly to mollusks, from less than one million years to more than 25 million years. The sudden appearance of new species in the record gave support the concept of rapid allopatric or peripatric speciation. Because both evolution in marginal populations and stasis in established species are old concepts, punctuated equilibrium (the combination of the two) seems to be more a new name than a new model.

In spite of the paleontologists' happiness with the standard model and the increasing popularity of punctuated equilibrium (at least among biologists), neither actually fits the geological record. Neither, in fact, includes a major feature of the record: the individual and independent disappearances of species from the record, the so-called background extinctions that leave sympatric species untouched and that are the standard mode of extinction in the long history of life on Earth. Whereas there is no dearth of explanations for mass extinctions (the simultaneous extinction of different taxa in different environments) no convincing explanation has ever been advanced for background extinctions.

With the advent of deep-sea drilling ships (1967), long and continuous sections of deep-sea sediments have become available. The oldest sediments retrieved from the deep-sea floor date from 180 million years ago. Deep-sea sediments contain a treasure-trove of microfossils common in the open ocean--especially Coccolithophorida (plated

protophytes) and planktic Foraminifera (shelled protozoans). Intercore correlation allows the reconstruction of continuous records of these organisms as they evolved through time. The longevity of coccolithophorid species was found to range, similarly to that of marine mollusks and Foraminifera, from less than one million years to more than 25 million years (average about 5 million years) (Emiliani 1982). Although most species appear and disappear abruptly, some lineages exhibit gradual phyletic evolution at rates that range up to millions of years (the *Turborotalia cerroazulensis* lineage, for instance) while some other lineages are seen to exhibit gradual evolution in one morphological character while exhibiting rapid evolution followed by stasis in another (the *Globorotalia conoidea* to *inflata* lineage--see Malmgren and Kennett 1981; Wei and Kennett 1988). If a rapid and repetitive environmental change takes place (as during the ice ages), species exhibit reversible morphogenesis (Emiliani 1969).

The deep-sea record shows that species originations and extinctions are individual events unrelated to other species in the same environment. Competitive replacement (a fitter species leaking out of a marginal environment and outcompeting an established species) is generally not observed. Most commonly, one or more new species, apparently related to an established species, sequentially appear in the record and coexist with the established species for up to several million years, thus increasing diversity; the established species may outlive one or more or even all of the new arrivals or it may be eventually replaced (but the replacement need not be better fit). Also, an established species may disappear without replacement, thus decreasing diversity. These events are clearly seen in innumerable stratigraphic charts, for instance those published by Postuma (1971), Stitt (1977--reproduced in Fig. 22.3, p. 485, in Emiliani 1992), Stainforth et al. (1975), and Bolli et al. (1985). Appearances and disappearances of established foraminiferal and coccolithophorid species during the past two million years are shown in Table 1.

TABLE 1

First and last appearances of foraminiferal and coccolith species during the past two million years.

<u>Species</u>	<u>Taxon*</u>	<u>Appearance</u>	<u>Time (years B.P.)</u>
<i>Globorotalia flexuosa</i>	F	last	68,000
<i>Globoquadrina pseudofoliata</i>	F	last	220,000
<i>Emiliana huxleyi</i>	C	first	275,000
<i>Globorotalia flexuosa</i>	F	first	401,000
<i>Globorotalia hirsuta</i>	F	first	450,000
<i>Pseudoemiliana lacunosa</i>	C	last	460,000
<i>Globorotalia tosaensis</i>	F	last	650,000
<i>Pulleniatina finalis</i>	F	last	1,400,000
<i>Globigerinoides fistulosa</i>	F	last	1,560,000
<i>Calcidiscus macintyreii</i>	C	last	1,590,000
<i>Gephyrocapsa oceanica</i>	C	first	1,680,000
<i>Gephyrocapsa caribbeanica</i>	C	first	1,740,000
<i>Discoaster brouweri</i>	C	last	1,950,000
<i>Globorotalia exilis</i>	F	last	2,100,000

*C = coccolithophorid; F = foraminifer. (Data from Berggren et al. 1985, and from Berggren W.A. and Berggren M., personal communication).

In 1981 I suggested that the sudden, individual disappearance of an established species could result from viral action (Emiliani 1982) (see also Emiliani 1992, 1993, 1993a). In fact, the extinction of an established species occurs when the species is abundant and well mixed (apparently facilitating viral infection and spreading); extinction is usually rapid (i.e., geologically instantaneous) and synchronous over vast areas; and the sympatric species are not affected. The recent discovery that viruses are extremely abundant in the ocean (10^6 - 10^9 viral particles per cubic millimeter) (Suttle et al. 1990) and that microplankton blooms are constrained by viruses rather than by lack of nutrients (Bratbak et al. 1993), adds strength to this model (which was named *extinctive evolution*) (Emiliani 1982). Extinction does not require that a virus exterminate a species down to the last individual--it is sufficient for the population to be thinned out sufficiently to impede gametogenesis. Some (e.g., Buckwold 1994) believe that, in order to survive, a virus has to "hide" in a host cell for which it is nonlethal. Not so in the ocean, where the standing crop of (continuously mutating) viral particles is astronomical.

It is now possible to construct a composite model of evolution from the concepts and the evidence discussed above. This model includes three principal modes: (1) slow to rapid phyletic evolution (generally applicable, but actually proved in nature only for some lineages of planktic foraminifera); (2) *extinctive evolution*--the viral (or microbial) extinction of an established, static species, with or without eventual replacement by a peripatrically-evolved new species (especially applicable to abundant and widespread marine invertebrates); and (3) the standard model, involving allopatric or peripatric speciation and competitive replacement of established species (especially applicable to scarce and scattered species, like land vertebrates). *Extinctive evolution* and the standard model rest on rapid allopatric or peripatric speciation followed by stasis.

The three modes are not mutually exclusive: phyletic evolution may occasionally be very rapid; the standard model may occasionally apply to abundant and widespread species; and *extinctive evolution* may apply to some scarce (but not widely scattered) species. Altogether, the three modes appear to be operating concurrently across the vast plexus of taxa and environments that expresses life on earth, with one or the other mode prevailing depending upon the circumstances, the taxa, and the environments.

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