PUNCTUATED EQUILIBRIUM AT TWENTY: A PALEONTOLOGICAL PERSPECTIVE

By Donald R. Prothero

"It was twenty years ago today
Sgt. Pepper taught the band to play..."

In many ways Niles Eldredge and Stephen Jay Gould taught paleontology to play twenty years ago, publishing a paper that helped revitalize the science. Long associated in the public minds with musty old bones, paleontology had the well-deserved reputation of being a stagnant backwater among the sciences.

Before the seventies, most college paleontology classes were little more than rote memorization of fossil names and anatomy. In his preface to the 1972 book Models in Paleobiology (where the punctuated equilibrium paper first appeared), Tom Schopf pointed out that a typical dissertation in paleontology consisted of describing some new fossils, with little thought about their broader theoretical implications, or about the possibilities for asking novel questions of the fossil record. Virtually all the paleontology textbooks of the time (such as the classic text by Moore, Lalicker and Fischer, first published in 1952) were simply compendia of fossils, and the broader theoretical issues were confined to few sketchy introductory chapters. The meetings of the Paleontological Society at the Geological Society of America convention were dominated by descriptive papers ("a new fauna from X" or "a new species of Y"), with only occasional broader theoretical papers that appealed to anyone other than the narrow specialist. This approach was called "stemp-collecting," since it focuses on studying the objects for their own sake. Others sneered and called it "stamp-collecting."

In the late sixties and early seventies, however, this situation changed radically. Perhaps the student activism of the sixties penetrated paleontology, or maybe the emphasis on ecology and holistic viewpoints were influential. In any case, a new generation of "young Turks" who finished their Ph.D.'s in the late sixties led a revolution that shook...
up the dusty old profession. They emphasized thinking of fossils as organisms, rather than dead objects to be described, catalogued, and put away in a museum drawer. In their papers and books, they applied ideas from modern biology—ecology, speciation theory, diversity and variation, population genetics, and many other concepts—to the fossil record. Although they recognized the limitations of the fossil record, they also found many instances where biological models lent new perspectives on long-studied fossils. Gould (1980a) called this the nonanthropic approach, since it seeks to find general, law-like properties among all the idiosyncratic details.

In 1971, David Raup and Steve Stanley published a radical new textbook entitled Principles of Paleontology. Unlike any paleontology text before (or since), it had no descriptions of fossil invertebrates; it was entirely focused on the theoretical issues of how we interpret the fossil record, and what we can (and can’t) learn from it. In 1972 Tom Schopf edited Models in Paleobiology (mentioned above), which contained a number of influential papers emphasizing new conceptual approaches to the fossil record. By 1974 Tom Schopf and Ralph Johnsen had founded the journal Paleobiology, which carried only papers of general theoretical interest; descriptive papers stuck to the venerable Journal of Paleontology. Since that time, the program of the Paleontological Society meetings has been packed with mind-boggling (and sometimes numbing) theoretical papers: abstracts of papers aimed at narrow specialists are rejected. Ultimately, the Paleontological Society recognized the influence of the generation of “young Turks” by establishing the Charles Schuchert Award for the outstanding paleontologist under the age of 40.

Although the original “young Turks” are now middle-aged, a new generation of paleontologists that they have trained or influenced dominates the profession. (My first freshman paleontology class in 1973 was taught using the brand-new Raup and Stanley text for the first time in my professor’s career.) Paleontology has been joined by Historical Biology, Lethaia, Palaeo, and other journals which emphasize papers of broad theoretical interest. More importantly, paleontology is no longer an intellectual backwater. Paleontological data and ideas are shaking up evolutionary theory. The controversy over mass extinctions (and whether they are periodic or extraterrestrially caused) has been written up in several best-sellers, made the cover of Time magazine, and stimulated the public...
debate about modern extinctions due to environmental destruction by humans. Dinosaurs are the hottest sad for kids of a certain age, although this rarely translates into careers in paleontology. (Like many paleontologists, however, I'm one of those kids who got hooked on dinosaurs at age 4 and never grew up.) Paleontology has always gotten front-page billing for amazing idiosyncratic wonders like giant dinosaurs, but now general, nonscientific ideas from paleontology are also influencing the rest of the scientific community. The earliest and most influential of all was punctuated equilibria.

The Birth of "Punk Eek"

Since his 1942 classic Systematics and the Origin of Species, Ernst Mayr has led the biological community in research in speciation theory. In 1954, Mayr proposed the allopatric speciation model. According to this idea, new species usually do not arise within the main body of a population, because the genetic exchange between organisms rapidly swamps any new variations. Instead, small subpopulations which are genetically isolated from the main population are more likely to change, because an evolutionary novelty has a much better chance of dominating a small population than a large one.

Many small populations, particularly those founded by a small number of settlers on an island, show the founder effect. The founders were a small subsample of the mainland population which may have had unusual gene frequencies (simply by accident of sampling), and all of their descendants will carry those genes. The founder effect need not be confined to islands, however. The Amish and Mennonites, who live among the rest of the American population but rarely interbreed for religious reasons, have many unusual genes.

Another possible cause is genetic drift. If a high percentage of genes are invisible to natural selection (as much research now shows), then they can randomly mutate without being weeded out. Ultimately, this random walk of mutation (or "genetic drift") can produce something which may...

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**FIGURE 1: COMPETING CONCEPTS OF EVOLUTIONARY CHANGE.**

A. The gradualistic model of shifting means of species characteristics through time (from Moore et al., 1952).

B. The punctuated equilibrium model, with static species already giving rise to new species through geological time (from Eldredge and Gould, 1972).
have a selective advantage—or may be deleterious. Either way, it has a much better chance of becoming dominant in a small population that is genetically isolated from its ancestors.

These populations are said to be allopatric, or living in "another homeland." If their isolation is long enough, they become so genetically different that when they are reintroduced or reinvade their original homeland (become sympatric), they can no longer interbreed with the ancestors; they have become a new species. This new species may die out quickly, or it may drive its ancestor to extinction, or both may persist side-by-side, typically by exploiting slightly different ecological niches. In paleontological terms, the allopatric speciation model predicts that species arise rapidly (a few hundred to a thousand years, but instantaneous in a geological sense) on the periphery of their range (where they are rarely fossilized). It predicts that the main pop-

ulation (most likely to be fossilized) will show little or no change, but will be suddenly invaded by new species with no apparent transitions between them.

Despite the harsh words of critics and derogatory labels (such as "evolution by jerks" or "punk eek"), the original formulation of punctuated equilibria was remarkably modest. As recounted by Eldredge (1985a) and Gould (1992), they were originally both graduate students at the American Museum of Natural History in New York. At the turn of the century the American Museum had once dominated vertebrate paleontology, but they came there to study with Norman Newell, who had an interest in evolutionary problems in fossil invertebrates. Both Eldredge and Gould found that tracing evolution in their chosen organisms (trilobites and land snails, respectively) was difficult; most of their fossils showed no change through thousands to millions of years of strata. In 1971, Niles Eldredge published a paper in Evolution which attempted to explain this apparent lack of change. Their joint paper published the next year in the Science volume, however, has been the focus of all the controversy.

Since the allopatric model had been dominant in biology for decades before Eldredge and Gould, it seems surprising that paleontologists ignored its implications for the fossil record. Some of this may have been inherent conservatism, or ignorance of biology, but it also had deeper philosophical roots. As Eldredge and Gould (1972) pointed out, paleontologists were raised in a tradition inherited from Darwin known as phyletic gradualism, which sought out the gradual transitions between species in the fossil record. They viewed species as part of a continuum of gradual change in anatomical characteristics through time. The classic metaphor showed each species as part of a bell-shaped frequency curve, with the mean shifting gradually up through time (Figure 1). Each species was thus an arbitrary slice through a continual lineage, and paleontologists agonized for years as to whether these arbitrary slices should be designated species. Indeed, this debate had its own label: "the species problem in paleontology."

Even their detractors concede that Eldredge and Gould were the first to point out that modern speciation theory would not predict gradual transitions over millions of years, but instead the sudden appearance of new species in the fossil record punctuated by long periods of species stability, or equilibrium. Eldredge and Gould not only showed that paleontologists had been out-of-step with biologists for decades, but also that they had unconsciously trying to force the fossil record into the gradualistic mode. The few supposed examples of gradual evolution were featured in the journals and textbooks, but paleontologists had long been mum about their "dirty little trade secret." Most species appear suddenly in the fossil record and show no appreciable change for millions of years..."
scale to be relevant to the debate, or too poorly dated to know anything about change through time.

For example, one of the main proponents of gradualism, Philip Gingerich (1976, 1980, 1987), showed just two or three examples of supposed gradual evolution in early Eocene (about 50-55 million years old) mammals from the Bighorn Basin of northwestern Wyoming. But a detailed examination of the entire mammal fauna (monographed by Brown, 1979, and Gingerich, 1989) shows that most of the rest of the species do not change gradually through time. Also, studies on specific lineages in restricted areas cannot account for the possibility that a gradual transition may actually reflect the migration of a dinally varying population across a region through time. This was documented by Schanklev (1961), who showed that some of Gingerich's patterns from the northern Bighorn Basin did not even hold up in the southern Bighorn Basin, just a few dozen miles away.

As Gould and Eldredge (1977) pointed out in their five-year retrospective on the debate, it's easy to pick one specific example of either gradualism or punctuational, but the important issue is one of generality. Which pattern is dominant among the species in the fossil record, since both are known to occur? If you sample all the members of a given fauna, which pattern is most common? In the

Figure 2. Evolutionary patterns at the Eocene-Oligocene transition (about 33-34 million years ago) recorded in strata near Douglas, Wyoming. On the left is the magnetic polarity time scale (Prothero and Swisher, 1992; Gradstein et al., 1992). In the middle are the ranges of species and families through the climatic shift discussed in the text. Most show prolonged stasis, followed by rapid speciation or extinction. All other mammals (not shown) exhibit no change through the interval. On the right are the climatic indicators which independently show that a major cooling event occurred at this time, even though most mammals did not track this climatic change. See text for discussion.

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twenty years since the paper, more and more case studies have been gen-
erated, and by now a pattern seems to be emerging (Gould, 1992; Stanley, 1992).

It is now clear that among micro-
scopic protistans, gradualism does seem to prevail (Hasumi and Ouawa, 1975; Scott, 1982; Arnold, 1983; Malmgren and Kennett, 1981; Malm-
gren et al., 1983; Wet and Kennett, 1986, on foraminifers); Kellogg and
Hays, 1975; Kellogg, 1983; Lazarus et al., 1985; Lazarus, 1986, on radiola-
rians, and Sorhannus et al., 1988; Fen-
nier et al., 1989; Sorhannus, 1990, on diatoms). As discussed by Gould and
 Eldredge (1977) and Lazarus (1983), this may be due to the fact that most
of these organisms are either asexual
clones, or show alternation of sexual
and asexual generations. Each clonal
lineage is distinct and many
never interbreed with other
lineages, so the issue of gene exchange
and homogenization may be moot. They
do not fit the genetic models that
biologists developed from complex
sexual organisms such as insects and
birds. In addition, they live in enor-
mos (trillions of individuals) popu-
lations that span entire oceanic water
masses, so they do not form many
small, isolated populations (Prothero
and Lazarus, 1980; Lazarus, 1983;
Lazarus and Prothero, 1984). Finally,
many of the morphological variants
that appear to be adaptations are due to
the same genetic lineage which responds
to di erent environmental conditions
with di erent anatomical features.
This is called ephiphenotypic variation,
and appears to be very common in
microscopic microorganisms. Perhaps
much of the morphological change
seen in microfossils does not reflect
any underlying genetic change, but is
simply an ephiphenotypic response
of the changing environment (Lazarus,
1983).

Among more complex organisms,
however, the opposite consensus has
developed. As paleontologists had known for over a century, most
species are stable for millions of years,
and change so rapidly that we rarely
witness it in the fossil record. Of the
hundreds of studies that have been
reviewed elsewhere (Gould and
 Eldredge, 1977, 1986; Gould, 1992), a
few stand out (Stanley, 1992). Cheetham (1986) and Stanley and
Yang (1987) examined all the available
linesages of their respective
groups (bryozoans and bivalves) through long intervals of time, using
multivariate analysis of multiple char-
acter states. Both concluded that most of their species were static through
millions of years, with rare but rapid
episodes of speciation. Williamson
(1981, 1985) examined the details of evolution of molluscs in Lake
Tornaka, Kenya, and showed that there
were multiple examples of rapid
speciation and prolonged stasis, but
no gradualism. Barnosky (1987)
reviewed a great number of different
divisions of mammals, from mam-
moths to shrews and rodents, that
lived during the last two million years
of the Ice Ages. He found a few
examples of gradualism, but many more
which showed stasis and punctuational
my own research (Prothero
and Shubin, 1983; Prothero, 1992;
Prothero, Heaton, and Stanley, in
press) examined all the mammals
with a reasonably complete
record from the Eocene-Oligocene (about
30-35 million years ago) beds of the
Big Badlands of South Dakota and
related areas in Wyoming and
Nebraska (Figure 2). This study not
only sampled every available lineage
without bias, but also had much bet-
ter time control from magnetic
stratigraphy (Prothero and Swisher, 1992)
and wider geographic coverage
than the studies by Gingerich cited
above. With one exception (gradual
swarming in the oreadont Minia-
chomys), we found that all of the Bad-
lands mammals were static through
millions of years, or speciated abrupt-
ly (if at all) punctuational
Contrary to claims by Hoffman
(1989, 1992) that the punctuated equilibrium model is either
wrong, false, or irrelevant, it has been one of the most
stimulating and provocative hypotheses in paleontology. With the
enormous literature it generated, or the fact that there have been several
recent symposia on the subject (e.g.,
Somit and Peterson, 1992) and twen-
ty-year retrospectives at national pale-
ontological meetings in Chicago in
July, 1992, and Cincinnati in October, 1992. Although a survey of the pro-
grams of recent meetings would show
fewer studies about evolutionary pat-
tens than a decade ago, there are still
many new studies with major new
insights being published every year.

Stasis, Landscapes, and Polyhedra

If the punctuated equilibrium model had merely shown that the bio-
logical species models could be
applied to the fossil record, then there
would have been little controversy
outside paleontology. The fossil
record would have just provided fur-
ther data for biological orthodoxy, as
paleontologists such as Simpson
(1944, 1953) did during the Neo-Dar-
winian synthesis of the 1950s (Gould,
1989; Eldredge, 1986b). In the 1960s,
evolutionary biologists often took an extreme panselectionist position. Nat-
ural selection was said to be constant-
ly acting on every tiny feature of an
organism, weeding out even the
smallest imperfection. Species are
arbitrary entities which constantly
track environmental change, like a
ball rolling across hilly terrain. Indeed, the popular metaphor of the
time was the "adaptive landscape."
Species were always trying to reach the "adaptive peaks" of the "land-
scape" and were continually modified in response to the shifting of the
peaks beneath them.
The discovery of stasis in most species for millions of years was an
fact that biologists did not expect (as
even Mayr, 1992, concedes). At first,
they dismissed it as genetic home-
ostasis or stabilizing selection
(Charlesworth et al., 1983; Levinton,
1983; Lande, 1985). But such models
are only appropriate on scales of a few
generations, or at most a few thou-
sand years. No environment is so con-
stant that stabilizing selection can act
for millions of years. This type of
explanation is typical of reductionist
evolutionary genetics (e.g., Dawkins,
1976), which treats organisms as con-
duits for genes, and even defines evo-
lution as "change in gene frequencies
through time." As Mayr (1992) points
out, such reductionism is now slowly
going out of vogue, as biologists real-
ize that organisms are integrated
wholes, with many different genes
interacting in complex ways.

More impressive are demonstra-
tions of species stability in spite of well
documented environmental change.
The fluctuations of glacial-interglacial
cycles during the last three million
years of the Ice Ages are about as
extreme a climatic change as our planet
experiences. Yet studies from land
mammals (White and Harris, 1977; Barnowsky, 1987) to microscop-
in most species in spite of these changes.

Rather than trying to test for adap-
tments, species migrate back and forth
in response to them.

My own research on the Eocene
Oligocene transition about 34 million
years ago (Prothero and Berggren, 1992)
documented another phenomenon.
Most of the mammals from the
Badlands discussed above (Prothero
and Shoabin, 1983; Prothero, 1992)
show remarkable stability over an inter-
val of well-documented climatic
change (Figure 2). Evidence from
palaeosols and land floras (Retallack,
1992) document a striking cooling
and drying event across this bound-
ary, with a woodland vegetation
(greater than 1000 mm annual precip-
itation) replaced by a wooded grass-
land (500 mm annual precipitation).

According to Wolfe (1992), mean
annual temperature declined almost
13°C and the annual range of tem-
perature increased dramatically from
3°C to about 25°C. Sedimentological
evidence from eastern Wyoming
(Evanoff et al., 1992) shows an abrupt
transition from moist floodplains to
semi-arid landscapes with abundant
wind-blown volcanic Ash. Most of
these events took place over a few
thousand years. This is certainly one
of the most severe climactic events
since the extinction of the dinosaurs.

Late Eocene land snails (Evanoff
et al., 1992) were large-shelled subtropi-
cal taxa now typical of central Mexico,
indicating a mean annual range of
temperature of 16.5°C and annual
precipitation of about 450 mm. In
the early Oligocene, these were replaced
by drought-tolerant small-shelled taxa
indicative of a warm-tempore dry
season. Reptiles and amphibians
(Hutchinson, 1992) show a trend
toward cooling and drying, with
aquatic forms (crocodilians, freshwa-
ter turtles, and salamanders) replaced
by land tortoises; size reduction in
turtles also indicates increased aridity.

In spite of all these changes, howev-
er, only one lineage of fossil mammal
underwent a gradual change. All of
the rest either remained unchanged
through the interval, or went extinct,
with new species replacing them.

None showed the panselectionist pre-
diction of gradually evolving to track
their changing environment.

If species are static through millions
of years in spite of environmental
change, then there must be some sort
of homeostatic mechanism that pre-
erves this stability beyond what tra-
ditional reductionists have assumed.
According to Mayr (1992), it is merely
the integration of species as complex wholes, so that
small-scale changes are insufficient to
upset the complex balance of integra-
ted genes. Others suggest that funda-
mental developmental constraints play
an important role in restricting the
possible avenues of change (Gould
and Lewontin, 1979; Kaufmann, 1983).

Still others suggest that there
might be properties of species that
may not have been discovered yet by
geneticists and evolutionary biolo-
 gist,s properties which operate on
scales of millions of generations and
years (Veha and Eldredge, 1984).

Instead of the "rolling ball" metaphor
so favored by evolutionary
biologists, perhaps species are more
like a polyhedron, which can
collide rapidly over from face to
face, but resists change when it is sitting on one
of its stable faces (Gould 1980).
Change only occurs when the thresh-
old necessary for it has been exceeded,
and then the polyhedron will resist
further change until that threshold
is reached again. Between stable states (the faces), how-
ever, the transitions are very rapid.

This kind of phenomenon is very sim-
lar to catastrophe theory (Schubert,
1992) and other theoretical models of
discontinuous change (Masters, 1992).

Species Sorting and
Macroevolution

The other major implication of the
idea that species are static for millions
of years is the implication for the real-
ity of species. Traditionally, species
were considered the sum of all their
component populations, and all
processes (such as selection) operated
on the level of individual and popula-

...palentologists have begun to shed their subservience to evolutionary biology, and assert the importance of the fossil record for detecting phenomena that are too large in scale for biologists to observe."

Traditional Neo-Darwinists have failed to see any difference between traditional natural selection and species sorting (Mayr, 1992; Hecht and Hoffman, 1986; Hoffman and Hecht, 1986; Hoffman, 1982, 1984, 1989, 1992). In reading the literature, it is clear that the debaters are talking past each other, each often working from fundamentally different perceptions of the world. Traditional Neo-Darwinists come from a reductionist viewpoint that cannot see species as entities, even after all the evidence that has accumulated. The opposing camp sees the world as hierarchically ordered, with each level having its own reality. As long as this fundamental difference in worldview undermines the argument, neither side will convince the other, even within the clearest possible examples.

More is at stake here than the reality of species, however. If species sorting is real, then the processes operating on the level of species (macroselectionary processes) are not necessarily the same as those operating on the level of individuals and populations (microselectionary processes). In other words, macroseletion may not just be microseletion scaled up. After decades of experiments on fruit flies, the most interesting evolutionary phenomena might only be studied in the fossil record, or in the embryology lab. With publications, prestige, and grant money on the line, the traditional research community of evolutionary biologists do not want to find themselves suddenly irrelevant to the most interesting issues in macroseletion. On the other hand, palentologists have begun to shed their subservience to evolutionary biology (Gould, 1983), and assert the importance of the fossil record for detecting phenomena that are too large in scale for biologists to observe (Gould, 1982a, 1982b, 1985; Eldredge, 1985b). Clearly, all of evolutionary biology is undergoing ferment and change. To paraphrase the old Chinese proverb, we indeed live in interesting times.
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