PUNCTUATED EQUILIBRIUM AT TWENTY: A PALEONTOLOGICAL PERSPECTIVE

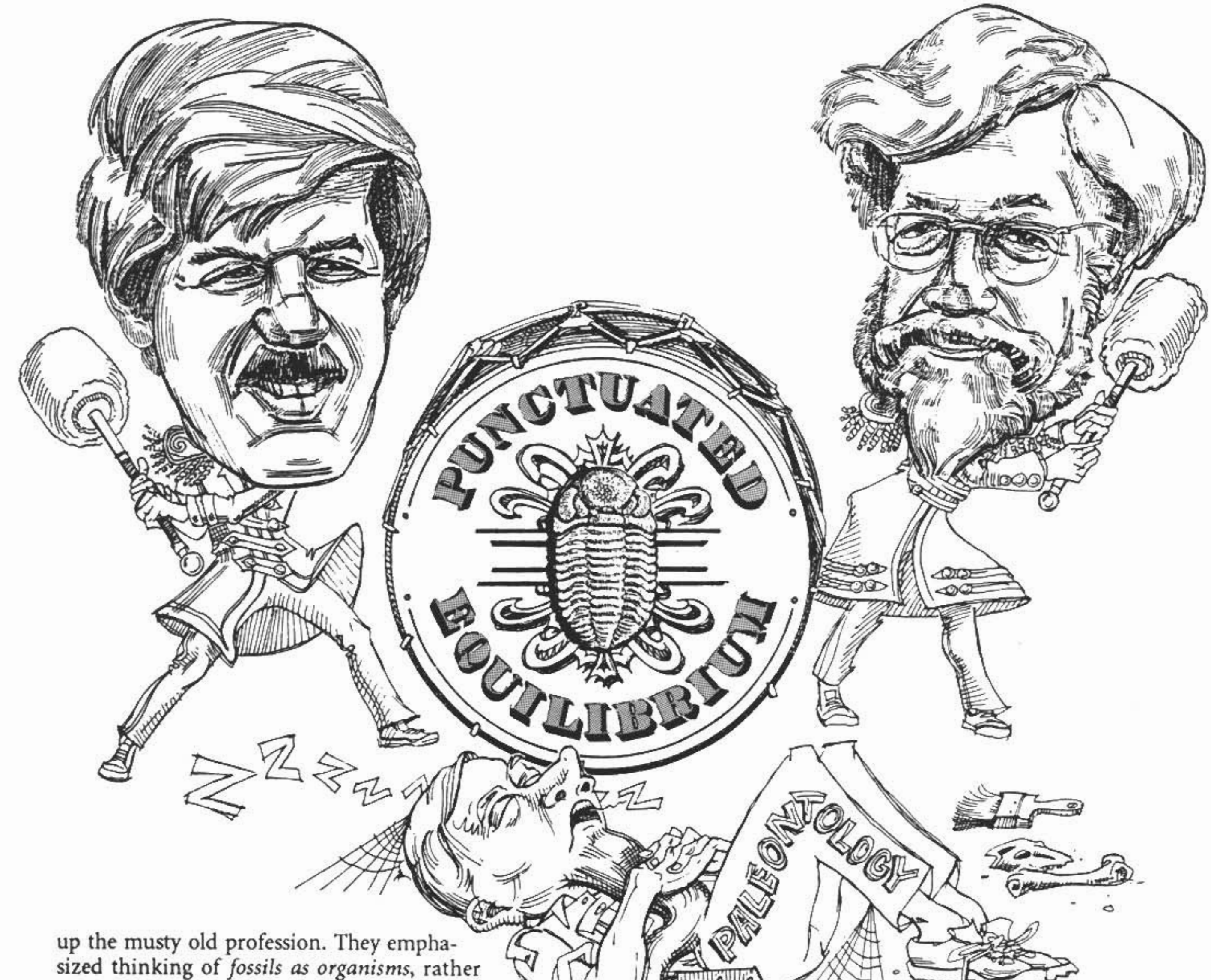
By Donald R. Prothero

"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 *idiographic* by Gould (1980a), 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 musty 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 *nomothetic* approach, since it seeks to find general, law-like properties among all the idiographic 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 1975 Tom Schopf and Ralph Johnson 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). *Paleobiology* has been joined by *Historical Biology, Lethaia, Palaios*, 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 fad 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 idiographic wonders like giant dinosaurs, but now general, nomothetic 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 subpopula-

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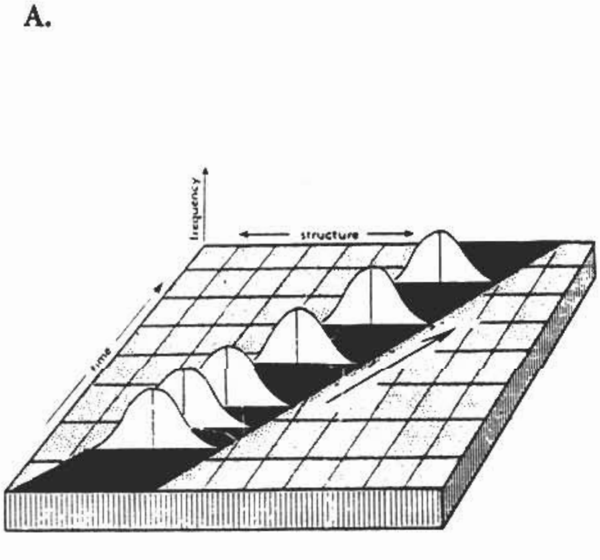
tions which are genetically isolated from the main population are more likely to change, because an evolutionary novelty has a much better chance of dominating a small population than a large one.

This can be due to several factors. 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



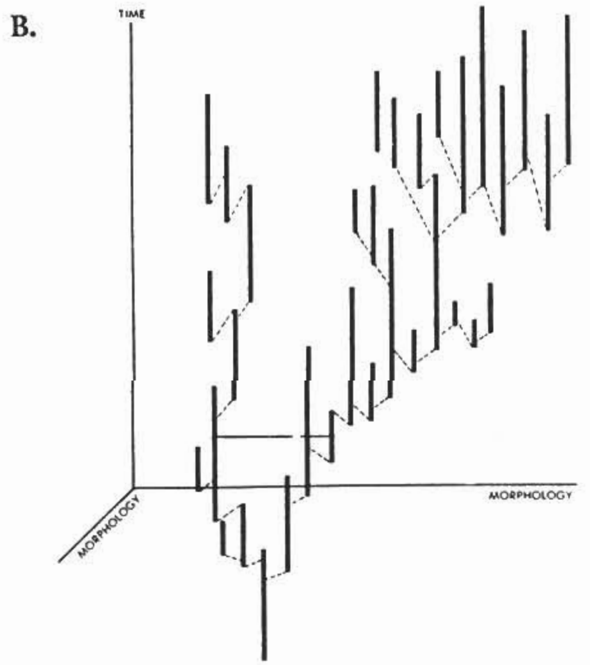


FIGURE 1. COMPETING CONCEPTS OF EVOLUTIONARY CHANGE.

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 abruptly 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 population (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.

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Despite the harsh words of critics and derogatory labels (such as "evolution by jerks" or "punk eek"), the original formulation of punctuated equilibria in 1972 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 Schopf 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 until their extinction.

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The Debate

When the punctuated equilibrium paper first came out, reactions were mixed. Since 1972 there have been many traditional paleontologists who denied its importance, and trotted out their favorite example of gradual evolution. Many of these "classic" examples were restudied in critical detail, and turned out to be ambiguous, or actually demonstrated punctuated equilibria better than gradualism.

There were a host of more trivial objections and misunderstandings, which have been discussed by Gould and Eldredge (1977) and Gould (1992). Most studies fell short because they focused on a single lineage (neglecting faunal variation) from a single section (neglecting geographic variation), often showing change in only one characteristic (neglecting morphological variation), which had not been analyzed by rigorous statistical methods. Other cases failed because they were on the wrong time 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 Bown, 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 clinally varying population across a region through time. This was documented by Schankler (1981), 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 punctuation, 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

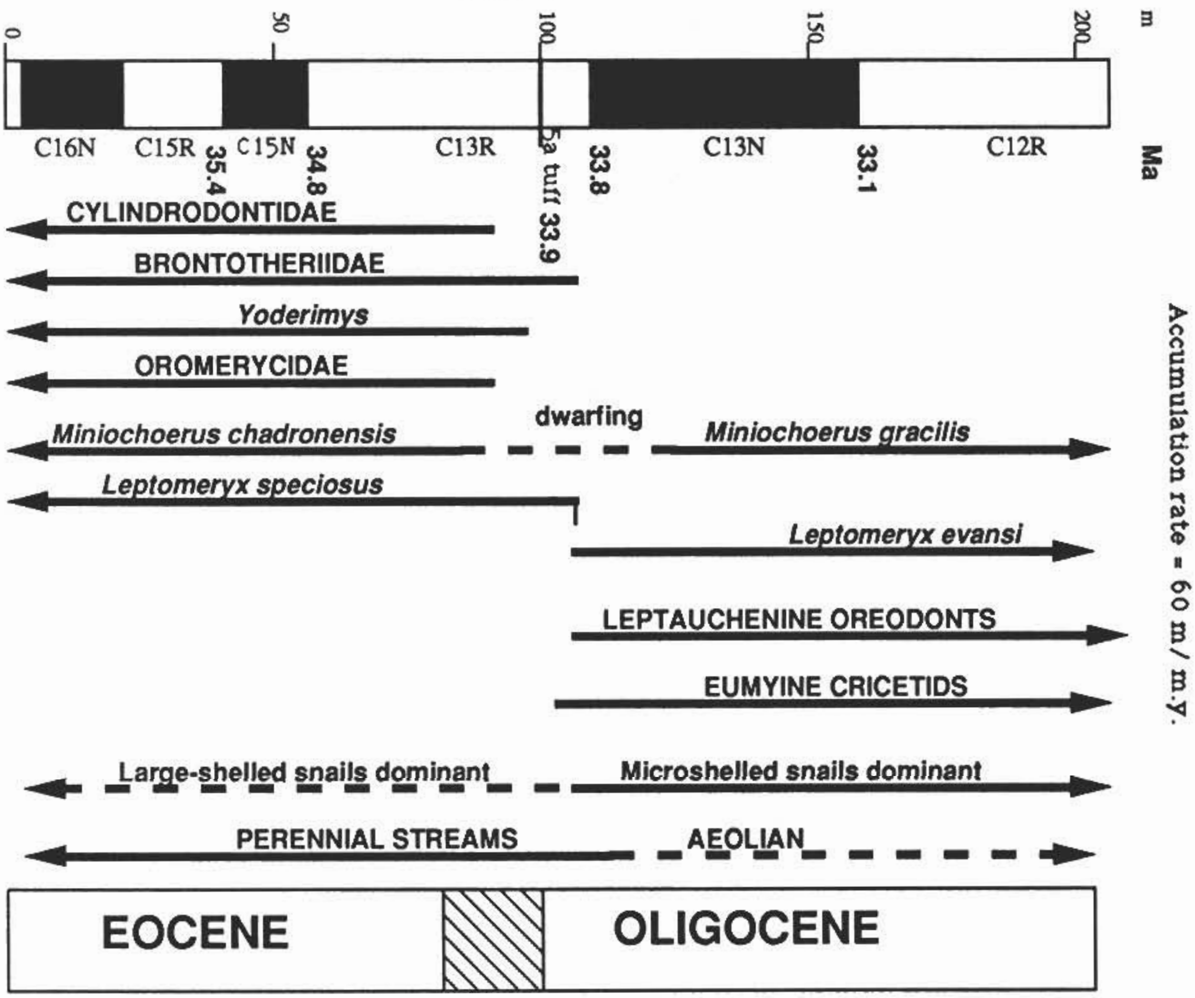

Figure 2. Evolutionary patterns at the Eocene-Oligocene transition (about 33-34 million years ago) recorded in strata near Douglas, Wyoming. On the left is the magnetic polarity time scale (Prothero and Swisher, 1992; Evanoff et al., 1992). In the middle are the ranges of species and families through the climactic 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 climactic indicators which independently show that a major cooling event occurred at this time, even though most mammals did not track this climactic change. See text for discussion.

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

It is now clear that among microscopic protistans, gradualism does seem to prevail (Hayami and Ozawa, 1975; Scott, 1982; Arnold, 1983; Malmgren and Kennett, 1981; Malmgren et al., 1983; Wei and Kennett, 1988, on foraminiferans; Kellogg and Hays, 1975; Kellogg, 1983; Lazarus et al., 1985; Lazarus, 1986, on radiolarians, and Sorhannus et al., 1988; Fenner 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 of sexual and asexual generations. Each cloning 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 enormous (trillions of individuals) populations 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 we call species may in fact be the same genetic lineage which responds to different environmental conditions with different anatomical features. This is called *ecophenotypic* variation, and appears to be very common in planktonic microfossils. Perhaps much of the morphological change seen in microfossils does not reflect any underlying genetic change, but is simply an ecophenotypic response to the changing environment (Lazarus, 1983).

Among more complex organisms, however, the opposite consensus had 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 lineages of their respective groups (bryozoans and bivalves) through long intervals of time, using multivariate analysis of multiple character 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 Turkana, 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 lineages of mammals, from mammoths 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 punctuation.

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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 better time control from magnetic stratigraphy (Prothero and Swisher, 1992) and wider geographic coverage than the studies by Gingerich cited above. With one exception (gradual dwarfing in the oreodont *Miniochoerus*), we found that all of the Badlands mammals were static through millions of years, or speciated abruptly (if they changed at all).

Contrary to claims by Hoffman (1989, 1992) that the punctuated equilibrium model is either trivial, false, or irrelevant, it has been one of the most stimulating and provocative hypotheses in paleobiology. Witness 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 twenty-year retrospectives at national paleontological meetings in Chicago in July, 1992, and Cincinnati in October, 1992. Although a survey of the programs of recent meetings would show fewer studies about evolutionary patterns 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 biological 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 further data for biological orthodoxy, as paleontologists such as Simpson (1944, 1953) did during the Neo-Darwinian synthesis of the 1950s (Gould, 1983; Eldredge, 1985b). In the 1960s, evolutionary biologists often took an extreme panselectionist position. Natural selection was said to be constantly 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 "landscape" 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 homeostasis 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 thousand years. No environment is so constant 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 conduits for genes, and even defines evolution as "change in gene frequencies through time." As Mayr (1992) points out, such reductionism is now slowly going out of vogue, as biologists realize that organisms are integrated wholes, with many different genes interacting in complex ways.

More impressive are demonstrations 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 climactic change as our planet experiences. Yet studies from land mammals (White and Harris, 1977; Barnosky, 1987) to microscopic marine ostracodes (Cronin, 1985, 1987) document extreme stability in most species in spite of these changes. Rather than adapt to new environments, 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) documents a similar phenomenon. Most of the mammals from the Badlands discussed above (Prothero and Shubin, 1983; Prothero, 1992) show remarkable stability over an interval of well documented climactic change (*Figure 2*). Evidence from paleosols and land floras (Retallack, 1992) document a striking cooling and drying event across this boundary, with a woodland vegetation (greater than 1000 mm annual precipitation) replaced by a wooded grassland (500 mm annual precipitation). According to Wolfe (1992), mean annual temperature declined almost 13°C, and the annual range of temperature increased dramatically from 5°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 volcaniclastic dust. 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 subtropical 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-temperate open woodland with a pronounced dry season. Reptiles and amphibians (Hutchison, 1992) show a trend toward cooling and drying, with aquatic forms (crocodilians, freshwater turtles, and salamanders) replaced by land tortoises; size reduction in turtles also indicates increased aridity.

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In spite of all these changes, however, 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 prediction of gradually evolving to track their changing environment.

If species are static through millions of years in spite of environmental changes, then there must be some sort of homeostatic mechanism that preserves this stability beyond what traditional reductionist Neo-Darwinism once postulated. Mayr (1992) argues that it is merely the integration of species as complex wholes, so that small-scale changes are insufficient to upset the complex balance of integrated genes. Others suggest that fundamental developmental constraints play an important role in restricting the possible avenues of change (Gould and Lewontin, 1979; Kauffman, 1983). Still others suggest that there might be properties of species that may not have been discovered yet by geneticists and evolutionary biologists, properties which operate on scales of millions of generations and years (Vrba and Eldredge, 1984).

Instead of the "rolling ball" metaphor so favored by evolutionary biologists, perhaps species are more like a *polyhedron*, which can roll rapidly over from face to face, but resists change when it is sitting on one of its stable faces (Gould, 1980b). Change only occurs when the threshold necessary to tip it over has been exceeded, and then the polyhedron will resist further change until that threshold is once again reached. Between stable states (the faces), however, the transitions are very rapid. This kind of phenomenon is very similar 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 reality 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 populations. But if species are not just arbitrary slices of a continuum, but distinct entities with their own history of "birth" (speciation) and "death" (extinction), then perhaps species have characteristics that operate on a *hierarchical level above that of the genes, the individual, or the population*. This concept of *hierarchy* (species are made up of populations, populations are made of up individuals, individuals are made up of genes, etc.) has important implications for evolutionary biology (Gould and Eldredge, 1977; Gould, 1982a, 1982b; Vrba and Eldredge, 1984; Salthe, 1985; Eldredge, 1985b; Gould, 1985; Vrba and Gould, 1986).

Although glimmerings of this idea were present in the original 1972 Eldredge and Gould paper, it first emerged explicitly in a brief paper by Stanley (1975) followed by his stimulating and controversial book Macroevolution (1979). Stanley called this concept "species selection," and it was the basis for a new round of debates for over a decade. Since the original proposal, Vrba and Gould (1986) have since argued that it should be called "species sorting," since the process is not really analogous to natural selection on the level of individual populations.

In a nutshell, the argument postulates that species are real entities which have characteristics that are more than the sum of the characteristics of their component populations. When two or more species come into competition, the differential survival which sorts out the "winners" and "losers" may be due to these intrinsic species properties, rather than natural selection on individuals or populations. The causes of the survival of a given species cannot be reduced directly to the survival of its component populations, but seems to be due to properties which are species-specific.

For example, the tendency of a group to speciate rapidly or slowly is not a property of its component individuals. Organisms do not speciate, species do. Elisabeth Vrba (1980, 1985) has suggested that the antelopes of Africa provide an example of this. The relatively conservative impala clade seems to have an intrinsically low rate of speciation. Only three very similar species in one lineage are known for the last five million years. By contrast, the wildebeest tribe has speciated profusely during the same period of time, with multiple episodes of evolutionary branching and extinction. Hansen (1978, 1982) argued that marine snails without planktonic larvae speciated more rapidly than those who disperse their larvae as plankton all over the ocean. The less mobile non-planktotrophic snails are more likely to be genetically isolated than species whose planktonic larvae spread their genes all over the ocean. Since the larval condition is a property of the species, not merely of its component individuals, it might represent an example of species sorting.

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Two groups of South American burrowing rodents, the tuco-tucos (genus *Ctenomys*) and the coruros (genus *Spalacopus*) both have evolved adaptations for a burrowing, gopher-like existence (Vrba and Gould, 1986). Tuco-tucos are far more speciose the coruros, even though they have the same ecology and home range. The difference lies in the fact that tuco-tucos have very low gene flow, so they can speciate rapidly, while coruros are genetically homogeneous. Other possible examples of species sorting were reviewed by Gilinsky (1986).

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, since each has 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 underlies the argument, neither side will convince the other, even with 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 (*macroevolutionary processes*) are not necessarily the same as those operating on the level of individuals and populations (*microevolutionary processes*). In other words, macroevolution may not just be microevolution 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 macroevolution. On the other hand, paleontologists 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 the paraphrase the old Chinese proverb, we indeed live in interesting times.

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