AST 309L—Lecture Materials, part II: Evolutionary processes; mass extinctions

Theory of evolution.

Although the empirical facts about evolution are well-established by now, especially the absolute and relative dates of appearance (and disappearance!) of various creatures, and the fossil evidence that small changes occurred over various time scales, there is no theory of evolution that is as well-developed as, say, the theory of stellar or even galactic evolution. Part of the problem is that biological organisms are immensely more complex than stars or galaxies, but also the fossil record is of course incomplete—there are bound to be gaps simply because of the chanciness of finding a certain fossil of a certain age; that is why this "record" is constantly being revised and filled in. Besides this, we cannot reconstruct fossil genomes, where the *real* evolution that gives rise to the body-size changes ("phenotypic" changes) occurs. However we *can* tell a lot about the historical relationships between organisms by comparing the sequences of (for example) bases in their genomes (see earlier notes).

Nevertheless, today's theoretical models of evolution have a lot in common with Darwin's basic ideas. Darwin basically theorized (not mathematically), by observations of lots of different organisms, that life has evolved over time by a process involving 1. Passing on of traits from one generation to the next, i.e. **inheritance** (he didn't know how this occurred, he just claimed that there must be some such process); 2. Some **variation** in the traits that are inherited (which we today attribute to mutations and other alterations of the genome); and 3. "**Natural selection**" in which some of these variations would be better fit than their ancestors, or other organisms, to cope with a changing environment, procure food, use chemicals to get energy efficiently, run fast, whatever it takes to live longer and/or reproduce more offspring. These "adaptive" traits would allow a larger fraction of organisms with these traits to survive to reproduce than those without these traits.

Today we know (since Gregor Mendel's genetics) that such a mechanism of inheritence does indeed exist, and we know about it in great detail: the genetic code. We also know that the processes giving rise to variation in traits are actually processes that cause changes in the genome, such as mutation, sexual recombination, transposable genetic elements, gene loss, gene duplication, and several other genome-altering processes. Modern evolutionary biologists think that most mutations are *not* beneficial, but are in fact "deleterious," but that the small fraction that *are* beneficial or advantageous are enough to allow natural selection to occur and cause adaptively useful traits to become "fixed" in a population. ("Fixed" means that the trait has spread throughout the whole species.) There exists a large literature of fairly complicated mathematical models that try to account for many experimental and real-world results concerning evolution. It is a long way from Darwin's necessarily rough ideas, but the basics are still there.

There are several other complications or even challenges to this broadly Darwinian theory of evolution.

1. Darwin thought that all evolution must be very gradual, by which he meant that changes must occur in tiny steps, and probably over very long time scales (what is meant by "long" is somewhat ambiguous). This "gradualist" view of evolution was challenged in the 1970s by the recognition that the fossil record often showed long periods (for a given species) during which apparently *no* evolution occurred ("stasis") and other periods when the rate of evolution was extremely fast ("bursts" of evolution). This type of pattern came to be called "**punctuated equilibrium**." It sounds like a theory, and is usually called a theory, but it is *not* a theory at all, simply observations of the fossil record. This doesn't affect the general Darwinian model of evolution, but it does require that any future theory of evolution must account for it. The degree to which punctuated equilibrium has occurred in nature is still debated today, and so is uncertain.

2. Darwin is usually represented as claiming that natural selection is based entirely on competition, but it is now recognized that other modes of interaction, e.g. symbiosis, cooperation, parasitism, etc. play a vital role. Things are more complex than initially thought, as in any subject.

3. Perhaps the most serious potential blow to modern Darwinian-type evolution theory was pioneered by the Japanese evolutionary biologist Kimura who claimed, based on extremely sophisticated mathematical models that most biologists of the time (and even today) could not understand, that most mutations were neither beneficial or deleterious, but were just "**neutral mutations**." He claimed that which traits get "fixed" in a population is mostly a matter of chance ("genetic drift"), with natural selection playing a minor role. At the time it appeared that his predictions of the degree of variation agreed better with data than theories based on natural selection. However by today selection models have become much more mathematically developed, and it is clear that both selective and neutral evolutionary processes occur, although there is still debate about which dominates (with most non-Japanese evolutionary biologists favoring selection of course). As discussed in class, there are many experiments today that perform natural selection "evolution in a test tube" for short-lived organisms like bacteria and yeast. Notice that, although people are often uncomfortable with modern Darwinian evolutionary theory because it seems "too random," Kimura's neutral evolution theory introduces a much more extreme form of randomness.

Students should consider which of these better favor the convergence of evolved traits (remember, our basic question is whether there has been a lot of evolutionary convergence, and if our kind of "intelligence" is one of the traits that we expect to have converged on other planets). (The same question should be asked of all the processes discussed in this section.)

4. A number of complications have been discovered that have altered and complicated our interpretation of evolutionary evidence. Examples include **exaptation** (change of function for some trait; e.g. insect wings might have once been selected for thermal insulaton, not flying); "**lateral transfer**" (sometimes called horizontal transfer), which means the transfer of genetic material between organisms, often of very different evolutionary descent (e.g. viral transduction of genes from one species to another); this process was apparently extremely rampant in bacterial populations on the early Earth;

epistasis, which refers to the fact that genes can influence neighboring genes, in various ways (that are not fully understood); the existence of genes whose function seems to be to increase the rate of mutation in times of environmental stress ("**mutator genes**" and genes that suppress "**heat shock proteins**"); these are believed by some to be closely related to cancer. In addition there are questions that are unanswered so far that have to do with the origin and benefit of having multiple chromosomes ("polyploidy"; bacteria are "haploids"), or meiotic sex (rather than mitosis). Generally, the genome is turning out to be a complex and dynamic entity, but there is nothing in this complexity that runs counter to the overall theme of inheritance with variation and natural selection.

5. The fact that extremely large changes in the environment have induced huge alterations in the direction of evolution on Earth has become more and more clear. The most prominent examples are the existence of mass extinctions, at least one of which was caused by an asteroid impact, and the increasing evidence that Earth has gone through some "Snowball Earth" episodes of nearly complete glaciation. We will return to these later, but for now notice that by producing huge stresses on organisms and creating multitudes of new niches to which creatures can (or can't) adapt, this part of the evolutionary process is much more *catastrophic* (meaning changes are sudden, not necessarily bad) than gradual (as Darwin had in mind). These large sudden environmental changes are also very chancy: How would the development of life on Earth been different if an asteroid hadn't wiped out the dinosaurs just when the mammals were in a stage of development that allowed them to survive and even dominate?

So the theory of evolution has become more sophisticated, but is not at the level where it can give us any indication of why the major events in evolutionary history (e.g. sex, the Cambrian explosion) occurred or whether they should expected on another planet. In that sense, there is still no well-developed theory of evolution, although few doubt that inheritance, variation, and natural selection have always played dominant roles, especially since there are so many examples that are seen both in nature and in the laboratory. A major problem is that we don't understand the relation between the genome and the traits, or "phenotype" that develops in a well-defined sequence in response to the genetic code. This problem of developmental (meaning: how development from fetus to adult is orchestrated by the genetic code) evolutionary theory is at the forefront of research today (often called "evo-devo"). In fact that is why decades ago Darwinian evolution was such an easy target—because people were wondering how phenotypes (observable traits) change without considering the genome as the driver of evolution. So connecting the evolution of genomes with the evolution of observable traits is the major unsolved problem in evolutionary biology. In a few cases there has been progress, but there is no overall "theory" of development yet. This is easy to understand once you take a single course in cell biology—even single-celled organisms are so immensely complex that it is difficult to make theoretical models for any of the amazing processes that occur.

More details on complications for the standard picture of biological evolution (most of these are processes that were mentioned above).

1. Punctuated equilibrium (this is *not* a "theory," just an interpretation of the fossil data.)

The arguments are based on morphological evolution (i.e. changes in form).

1. "Sudden"appearance of new species. "Bursts" of evolution? Or just migration or competitive exclusion and re-migration?

Is 30,000-50,000 years "sudden"? It's still thousands of generations. Nov.30 1988 Nature, paper by Adrian Lister--pygmy deer evolved from local red deer 6 times larger on an island off the coast of France in ***less*** than 6000 years, i.e. roughly a few hundred generations. Examples like this are now common.

2. Long periods of "stasis"--no evolution at all over millions of years or longer. Much greater stability than the traditional gradual Darwinian theory predicted. Do mutations *stabilize*? Why do some species *not* evolve for such long periods of time?

Neo-Darwinists sometimes appeal to mosaic evolution--different parts of an organism do not change at the same rate—to explain the “appearance” of punctuated evolution. A creature can resemble its ancestral organism in some respects, descendents in others. e.g. Archeopteryx (bird/reptile?), australopithecines (ape/hominid?). So according to this idea, if you follow a single trait in the fossil record, long periods of little change may appear, but not because evolution is not occurring. [But these periods are *very* long!] Today not many people believe that this can be the explanation, and evolution with bursts and long periods of stasis are accepted at least in some cases.

Another problem with the punctuated equilibrium scenario is that Neo-Darwinists define "species" in terms of inability to cross-breed ("reproductive isolation"), *not* morphological differences. Morphological evolution and reproductive isolation are distinct, and can occur together or separately. Morphological evolution might occur as response to environmental challenges (e.g. new predators, new habitat), while splitting into new species might occur as a consequence of spatial isolation (for example).

And so the debate over punctuated equilibrium interpretation of the fossil record has continued, but the interpretation has become stronger and stronger, especially when such evolution can be observed in bacteria evolving in laboratory conditions.

[Note: Nothing on this page is required reading; it's just here in case you're interested.]

The issue of punctuated equilibrium vs. gradualist models in evolutionary biology is just the tip of an iceberg of thought on the nature of change in various areas. Sudden or rapid change has always been contrasted with slow, gradual change ("uniformitarianism") in various theories of geological, ecological, political, social, and cultural development. A sample of the many papers on aspects of punctuated equilibrium that appeared in the issue of *Journal of Social and Biological Structures* (1989, vol.12) that is interesting in this regard is listed below. If you found a way to track the citations to these articles in one of the UT web search engines, you could see that the issue still engenders strong debate, from historians to biologists.

"Punctuated equilibrium: the view from the elephant", by A. Somit and S. Peterson (pp.105-115)--discusses implications of punctuated equilibrium view of biological evolution for the social sciences, and the emergence of biologically-oriented approaches to subfields in sociology, economics, political science, archaeology, and law.

"Gradualism and discontinuous change in evolutionary theory and political philosophy", by R.D. Masters (pp.281-301)--examines history of views of change in biology and in human history and politics, and how they have been related, going back to Aristotle, Lucretius, Rousseau, Hobbes, Marx,...). Concludes no clear correlation and hence no inherent political bias to either model for biological evolution.

"Punctuationalism in societal evolution", by K.E. Boulding (pp.213-223).

Also see the papers on the empirical case for the punctuated equilibrium model and its problems by Stanley (p.159), Gould (one of the originators, with Eldridge, of its most recent incarnation, p.117), and Mayr (one of the "fathers" of and most respected researchers in evolutionary biology, p.137)

Consider how change appears to you, in various aspects of your own life, say, or in developments in contemporary culture, etc. If you think "gradual" vs. "discontinuous" is a misleading distinction in these cases, why has it continued to provoke so much debate? (It is related to questions of "being vs. becoming"; "free will" or chance vs. determinism; "order vs. chaos"; etc., etc.)

2. Neutral evolution theory: Most mutations that become fixed and significant are "neutral", not advantageous. Evolution just consists of random statistical fluctuations ("*genetic drift*") unassociated with natural selection. Major proponent is Matook Kimura (major book is *The Neutral Theory of Molecular Evolution* 1983).

Evidence:

a. Amount of genetic variation within given generation is much larger than expected by natural selection. Large variation suggests that most genetic differences neither help nor hinder an organism's survival--persistence or elimination of these differences is a matter of chance.

b. Rate of genetic change is fairly constant over long periods and is about the same in different species. The traditional synthetic theory of evolution implies *variable* rates of molecular evolution, because selective pressures vary over time and from species to species. (Rebuttal: What matters is the *function* of the gene, which may be constant.)

For major criticism of neutral evolution, see Gillespie, J.H., *The Causes of Molecular Evolution* (1991). Today these warring factions have reached a sort of agreement that both neutral and selective evolution occur in different organisms, or even in different genes of the same organism.

3. Directed mutation? (Answer: No, but mutator genes! i.e. genes that can cause the mutation rate to increase drastically.)

"Directed mutation," the idea that an organism can change its genome during its life (not just pass variation to descendents) due to response to the environment, would be the most heretical of ideas, if correct. It is kind of the reverse of the neutral theory, and contradicts a basic tenet of evolutionary theory: that information can only flow from genes to proteins (genomes to phenotypes if you like).

1988-1990--two independent papers in respected refereed journals (Cairns *et al*., *Nature*; Hall, *Genetics*; but Hall later dismissed the mechanism he proposed) presented evidence that organisms can respond to environmental stress by reorganizing the genetic material *in a purposeful way*; not by random mutations with improvements surviving. (From the Cairns *et al*. paper: "cells may have mechanisms for choosing which mutations will occur.") This is equivalent to arguing that the environment directs the evolution of new species, and carries a "Lamarckian" implication that organisms can adapt their genes to suit a new environment. (However note that no one is claiming that *all* or even *most* mutations are nonrandom, just that some are.)

This would also destroy the belief that organisms are related to some ancestor if they share traits; instead they may just share exposure to the same environmental changes. So evolutionary trees based on molecular traits would need extreme revision.

Directed mutation would also challenge the "central dogma" of molecular biology: that information transfer in cells only goes from DNA (and RNA) to proteins, not the reverse.

But many believed that the experiments don't require such radical solutions, and some think that they can be explained by well-documented aspects of bacterial metabolic regulation (see MacPhee, *American Scientist* , v.81, p.554 [1993]). The answer appears to be somewhere in between. Nearlyall recent work interprets the effects as the result of a previously-unknown kind of gene: "**mutator genes,**" which "switch on" only when organisms are subjected to extreme stresses, and whose effect is only to greatly increase the mutation rate. **<u>These genes therefore provide a huge amount of genetic diversity (large mutation rate) just when needed</u>**.

Some of these "hypermutation" effects, for example the rampant mutation related to whether the so-called "heat shock protein" p53 is expressed or not, are known to be related to cancer in mammals. That is why a lot of cancer research has to do with experiments involving genetic changes in microorganisms—humans actually share a lot of DNA repair machinery with microorganisms, which is just one example of why it is hard to escape the idea of a connected "tree of life."

So although virtually no one believes that directed evolution occurs, the possibility spurred so much research that other new mechanisms were discovered that can greatly increase the diversity of genomes, and hence can speed evolution. The role of these processes in long-term evolution is currently unknown.

4. A few significant additions to traditional evolutionary ideas:

a. **<u>Exaptation</u>**--features that have evolved for one purpose are often exploited for very different purposes. Now thought to play at least as important a role in evolutionary change as adaptation. (See Gould and Vrba 1983 *Paleobiology*,v.8,p.4). Notice how "fluky" this might be. Example: organs of flight in insects may have originally been selected for as organs of thermal exchange. (See Kingsolver and Kochl 1985 *Evolution*, v.39,p.488.) Also feathers in birds. Compare functions of thought and reasoning today to possible original context. Or brain's "reading circuits".

b. **<u>Viral transduction</u>** ("gene smuggling")--viruses can transfer genetic material, even between species; e.g. development of eye in squid and in vertebrates might *not* be independent parallel evolution, supporting convergence, but just due to viral transduction. [This is an extreme and speculative example to get the point across.]. (There are at least two other processes of "**<u>lateral transfer</u>**" that occur in bacteria, but it isn't known how these processes might affect evolution of complex traits in "higher" organisms. Lateral transfer almost certainly was a dominant mechanism in early evolution of microorganisms.)

c. **<u>Transposable genetic elements</u>**—genetic hitch-hiking, jumping genes, transposons, and chromosomal rearrangements can result in sudden and dramatic changes in genetic structure (McClintock 1984 Science, v.226, p.792 was among the first to suggest this). Instead of a "point mutation" involving a single nucleoside, an entire cluster of nucleotides or genes is shuffled among chromosomes. This means that genes lying close on a DNA strand to a mutation that eventually proves to have survival value (or be deadly!) may also be selected, even though those genes are not "adaptive" at that time.

There are more processes that are undoubtedly important that we don't have time to examine. **Gene duplication** (and even whole genome duplication) is now recognized as an extremely important process (although no one really understands how it occurs); this process was proposed as the driver of evolution about 1970 by Ohta, but has taken decades to be accepted.

Recombination is an extremely common and potent process, whereby parts of two DNA strands join up "end to end." (Look it up if you don't know what it is—it is the basis of sex in a general sense, and is well-understood in a descriptive sense.) G. Levinson (1994) found, using computer simulations, that recombination is more potent than mutation as a source of evolutionary change, because the resulting genome changes are faster and because it provides a way to avoid “mutational meltdown” by accumulated deleterious mutations. (Don’t worry about this technical terminology if you aren’t interested; if you are, look it up if you want details.)

Example of how all this is related to our basic question in this course: b. and c. above result in sudden changes in genetic structure (which could account for "punctuation" [see below] in the fossil record), and show how evolution can include characteristics that were not themselves selected for "reproductive fitness" ("survival value"). b. above could be used to explain away apparent convergence of traits in otherwise disparate species.

-------> These all add considerably to the randomness, or "serendipity" of evolution. They might lend support to Kimura's neutral theory of genetic drift, at least as part of the story. They make evolution look even less "purposeful" than adaptation did!

This suggests that evolution occurring on another planet (or if earth's history were to rerun its course) is **extremely** unlikely to result in a species resembling ours (consider "intelligence").

------>***But you could argue the opposite view*****:** networks of connected excitations (e.g. neurons w/ axons and dendrites) developed in *most* species, and evolution is mainly the increasing complexity of such networks (e.g. the modular nature of cell structure, brains with localized functions, ecological systems, communities, cultures). All the discussion about other morphological features (like wings or eyes or bipedalism...) is just about details. This is how you would argue for convergence even in the face of these seemingly random or at least highly probabilistic (i.e. chancy) processes. Maybe all these processes lead in the same direction: the formation of more and more complex networks and functions they can carry out. You will be reading more about whether or not complexity is inevitable in ouside readings.

Mass Extinctions

Best-known: dinosaurs, 66 Myr ago (Cretaceous-Tertiary boundary). But many other "mass extinctions", in which a large fraction of species went extinct, have occurred (see graph in text, others shown in class). Greatest mass extinction was about 250 Myr ago. The occurrence of these events *seems* to be **periodic**, with period of 26 Myr, but still disputed.

1979--Alvarez's et al. found <u>iridium</u> enhancements in rocks at the Cretaceous (e.g. dinosaurs, conifer trees]-Tertiary [e.g. mammals, flowering plants] boundary. Iridium is nearly absent from earth's crust--it was dragged into core with iron early in earth's history, but *is* relatively abundant in certain kinds of meteorites. The suggested that iridium settled out of global dust cloud due to impact of 10 km diameter meteorite. (Calculated from mass of 1/2 million tons needed to account for abundance in the rocks.) Impact speed would be 45,000 mph. Dust cloud blocked sun, cooled planet, killed dinosaurs and 75% of other species. This is the <u>*meteorite impact theory*</u>. (Problem has been that the cloud particles should have settled in only about 6 months: too short for extinction. See below.)

<u>More evidence for meteorite theory</u>:

1. Iridium excess at about 100 sites (of the same age) all over the earth.
2. Excess abundances of other heavy elements in the same layer, with abundances similar to those in meteorites.
3. Signs interpreted as meteorite damage (mostly "shocked quartz" [seen only at meteor craters and nuclear explosions], change in crystal structure [very rare, even at meteor craters], and tektites; "droplets" that form when solids cool and solidify while still in the air).
4. Where's the crater? The 110 mile diameter crater found in 1991 in the Yucatan peninsula (beneath town of Chicxulub) is now believed to be the "smoking gun" because the subsequent (1992) age determination gave 65 Myr!

Evidence that the "great kill" was preceded by series of smaller extinctions, and the evidence for small craters, suggests *multiple impacts*----> meteorite swarm? fragments from richochet? In June 17 1993 Nature, Robin et al. give evidence for 2nd object that splashed in northwestern Pacific Ocean at about 65 Myr ago (from particles found in seafloor sediments; they are iridium-rich). Schultz proposed angle of impact was $<10^o$, fragments richochet into ring around Earth, blocking sunlight, gradual descent of impact debris kills off the rest of the non-survivors.

Effects:

1. Plume of vaporized rock--shock-heats atmosphere, “broiling” the surface, causing extensive wildfires.

2. Acid rain-- the heating by the plume causes N and O to combine with water vapor, producing nitric acid, which rains out in concentrated form. Nitrous oxide dissolved in oceans would be responsible for much of marine extinctions, acid rain would kill vegetation and acidify lakes.

3. Heating of atmosphere (by friction of rebounding fragments) leading to global wildfires (as in a broiler). Some people have claimed that a shift in the carbon isotope ratio at K-T boundary could in part be due to burning of 25% of land vegetation.

4. Greenhouse effect (heating) due to CO_2 releleased by the impact. O’Keefe and Ahrens (1989...) shoot steel balls into different types of rock at 4,500 mph, measuring CO_2 released. They find that a 10 km. asteroid would increase CO_2 by 2-5 times almost overnight.

5. Dust and smoke in the atmosphere reduces sunlight for up to a year, resulting in a sudden and severe “global winter.” This would have stopped photosynthesis for up to a year, resulting in extinction of many key organisms in food chains.

6. Also a tidal wave a mile high would have traveled from Gulf of Mexico through southernmost states, ~1,000 km inland.

Note: A major problem has been that it’s hard to see how the extinctions could be due to cooling from suspended soot particles in the atmosphere, because the calculated settling time is only about 6 months. A study by Baines et al (JPL) suggested that sulfuric acid could have dropped temperatures to near-freezing (because of it’s high albedo--reflects lots of sunlight) for decades, and this would have been the impact-induced cause of the dinosaur extinction; and *only* because this region in Mexico where the impact occurred is so sulfur-rich--otherwise, there’d still be dinosaurs!]

A major result was the 16-inch core of mud from the ocean floor in March 1997 by Corell, Norris et al., which shows the time line of the extinction 65 Myr ago in better detail. Can see fossil-rich (before impact) white layer at bottom, gray-green section with impact debris, reddish stripe with iron-rich remains of the asteroid or comet, then layer with few fossils, then abundance of fossils occurring at top. Norris estimates 5,000 years passed (rapid!) before life recovered, but very uncertain. See also article in Nature v. 414, p. 861 (2001) for more recent work. Huge number of papers since then have continued to fill in details.

Competing (and traditional) theory: ***massive volcanic eruptions***. Get sulfur dioxide, acid rain, longer-term global greenhouse... And there *is* evidence for a series of huge lava flows in India that date to K-T times. Also, iridium *has* been found at Hawaiian "hot spot" volcanos. Shocked quartz could arise in magma chambers. But the periodicity of 26 Myr (see below), if real, is hard to understand with this theory. Of course, maybe there is no periodicity.

Recent attempts to reignite volcanic explanations: Antipodal (opposite side of earth) volcanism by impact-- 1994 paper by Hagstrum et al. (But this could also be in part a tendency of traditionalists to keep trying to salvage the volcanism theory.)

Several proposals that massively erupting volcanoes as the trigger for some mass extinctions have appeared. The best evidence is the new (Kamo et al. Sept. 2003) age of 251.1± 0.3 million years for the Siberian Traps eruption event, exactly at the uranium-lead age for the largest mass extinction, the Permian-Triassic, as determined in 1998 (Bowring).

The idea that an impact triggered massive volcanic eruptions is sometimes called the "double-whammy" theory for mass extinction. This was claimed for several years concerning the "dinosaur extinction" at 65 million years ago, but recent more precise dating of the Deccan traps of India (where the volcanism took place) shows that the eruption came half a million years too soon to trigger the extinction. But maybe greenhouse gases from the eruption set off the warming recorded at that time, which could have weakened the biota *before* the impact. What if mass extinctions require a "weakening event" shortly before an impact? One thing now seems certain: the "dinosaur" impact did NOT trigger great volcanic eruptions. (See Science v. 302, p. 1315 [Nov. 2003].) However the biggest of the mass extinctions at 251 million years ago now has evidence both for impacts and for volcanoes!

Both theories return to *catastrophism* instead of *uniformitarianism.*

There are still other ideas for mass extinctions. A recent paper claims evidence that the "Ordovician mass extinction" about 400 million years ago was due to a nearby (half-way across the galaxy) gamma-ray burst event! The radiation is supposed to have destroyed the ozone layer (allowing in orders of magnitude more UV radiation), resulted in serious acid rain, and possibly darkened the skies for months to years to to formation of NO_2.

Besides their apparent randomness, consider how studies of the details of the extinction sequences have implications for evolutionary theories. For example, in an April 21 1995 Science article, Jablonski and Ray found that for the mass extinction at the end of Cretaceous period (65 Myr ago), survival chance didn't depend on body size or feeding strategy or habitat. Would speculations based on "natural selection" have expected anything like this?

Interest in and public concern about impacts has been fueled by the appearance of bright comets (e.g. Hale-Bopp, spring 1997), the 1994 collision of comet Shoemaker-Levy 9 with Jupiter, and continuing reports of asteroidal "near misses". On Feb.9 1997 NBC presented a made-for-TV movie about such a catastrophe; it was preceded earlier in the week by a segment of "documentary" NBC Dateline (edited from a NOVA documentary) on the subject (that was clearly a promo for the TV movie).

And don't forget those great movies like "Armageddon."

But there *is* a finite probability of an impact in the near future and several groups are devoted to watching for incoming asteroids. There were a few "near misses" in the last couple of decades.

Periodic extinctions? (graph shown in class; see text for different-appearing graph over smaller timescale)

Raup and Sepkoski studied extinction record of 3500 families of marine organisms, then 11,000----> 26 Myr period? (Very difficult to establish periodicity in noisy data!) See D.M. Raup book *Extinction: Bad Genes or Bad Luck?* (1992; role of catastrophes, mass extinctions, etc.) for semi-popular account in much more detail. [Very recent book by P. Ward named *Future Evolution* brings much of this up-to-date and contains a controversial suggestion about the future.] Note that the 250 Myr- ago extinction was the most severe; some estimate 96% of marine species went extinct.

The extinction study report was followed by claims in 1984 that craters on Earth had ages consistent with a 30 Myr periodicity. This is as difficult to establish as the periodicity of the extinction data, and I am unable to ascertain how likely this is regarded today. (If a geologically-inclined student tries to find out, please send me an email!)

All proposed explanations for periodicity rely on perturbing Oort comet cloud, releasing a large flux of comets that head toward the inner solar system. This is an old idea (Oort 1950), but until the 1980s, people thought the perturbations occurred randomly as the result of passing stars or clouds.

But now what was needed was a process for *periodically* perturbing the comet cloud.

1. Solar system's vertical oscillation through galactic plane. This could cause:

a. Impulsive, intermittent perturbations of the comet cloud by large interstellar clouds.

b. Alterations in the comet flux due to tides exerted on the Oort cloud by the matter in the Milky Way: Either "disk tides" (perpendicular to plane of galaxy) or "distant matter tides" (within the plane of the galactic disk, due to the entire galaxy, including our galaxy's core).

2. Tenth planet, beyond Neptune, highly eccentric and inclined orbit. Would continuously perturb the Kuiper belt (inner comets), with about 5 Myr modulation. Unlikely—if massive enough to do this, we'd probably have seen it.

3. Sun has a faint, dwarf companion---> "<u>Nemesis</u>". Orbit would have to be very eccentric. It would produce a single brief shower per cycle. This would be extremely difficult to discover because of its faintness and slow motion. Searches over the past 20 years have not given any evidence for it.

Most of these suggestions met with substantial problems during the late 1980s. In 1995-1997 Matese, Whitman, et al. finally carried out calculations for the "disk tide" effect (1b above) and found that the comet flux could be varied by a factor of four by this effect. Later work suggested that the "distant matter tides" may contribute about 1/3 of the Oort-cloud comets. (Perturbing effects of nearby stars and giant interstellar clouds turns out to be a tiny fraction of the total.)

But some disagree with the periodicity interpretation of the data, others with the idea that meteorite impacts were the dominant cause, etc. For example, as far as I know, iridium excesses have been found at only one other extinction layer (34 Myr). And more recent reconstructions of extinction rates do not look so periodic, although they certainly all show the largest peaks.

By now there are *thousands* of papers on this subject, so it's difficult to make sense of it. Your textbook avoids the question of periodicity, but does give a good discussion of the importance of mass extinctions for life and evolution.

Some more recent developments:

August 1998 Geology. Morokweng crater found beneath the Kalahari Desert in NW part of South Africa. Age =143-148 million years. This is very close to the age estimated for the end of the Jurassic era at 145 million years, so this might explain the mass extinctions among reptiles and marine life at that time.

➡But there is also evidence for large impacts *without* much extinction:
July 24 1998 Nature: Bottomley et al. date a large Siberian crater (Popigai) at 35.7 Myr, very close to age of a crater recently discovered beneath the Chesapeake Bay. Yet no rise in extinction rate. (Next major extinction came about 2 Myr later).

More recently yet:

➡June 2003 (Science 300, 1734) Ellwood et al. claim evidence from shocked quartz, elemental and isotopic anomalies, microspherules, and more (in rocks found in desert near Rissani, Morocco), for a bolide impact in the mid-Devonian about 380 million years ago, coincident with a major global extinction event (Kacak/*otomari* event), in which as many as 40% of living marine animal general were wiped out. For reply to criticism and more evidence see 23 Jan 2004 Science, v. 303, p. 471.

➡November 2003 (Science 302, 1388; see p. 1314 for summary)—Basu et al. claim evidence from meteorite fragments found in Antarctica for a bolide that impacted Earth about 250 million years ago, coincident with the biggest of the "Big Five" mass extinctions at 251 million years. These are nontraditional impact markers that not all "impact geologists" accept. (See commentary on p. 1314 of above reference, which explains various imact markers and their problems.)

2004: papers appear that refute evidence for impact as cause of the 250 Myr extinction.

<u>Conclusion</u>: There is no agreement about the importance of impacts, except probably for the 65 Myr ago ("dinosaur") extinction. Impacts *may* have been responsible for some other mass extinctions but the case here is weaker.

The upshot of all this is that mass extinctions HAVE occurred many times in the history of the Earth, and whatever their cause, **they emphasize the "contingency" of evolution**—they are basically severe random effects. If the emergence of mammals as dominant creatures depended on the demise of the dinosaurs, then what are the chances that mammals like us would arise on another planet? On the other hand, the random catastrophes that were mass extinctions must have also presented huge challenges that might have been decisive in causing evolutionary change, so it might be unlikely that such extreme evolutionary development could have occurred without mass extinctions! Like most evolutionary processes, they give and they take. Notice also that the importance of such events is consistent with the impression of the fossil record as consisting of "punctuated equilibrium."