Paleontology and the History of Life

Michael Benton

And out of the ground the Lord God formed every beast of the field, and every fowl of the air; and brought them unto Adam to see what he would call them: and whatsoever Adam called every living creature, that was the name thereof.

Genesis 2:19

People have always been astounded by the diversity of life, although perhaps in different ways. In prescientific times farmers saw how their crops and livestock were merely part of a much larger richness of life, and people have always striven to understand the complexity and arrangement of living things. From Aristotle to Linnaeus, scientists attempted to catalog life and to understand where it had come from. During the eighteenth century it became clear to all savants that the earth had been populated formerly by strange and marvelous creatures that had since become extinct. By 1820 some rough picture of the succession of floras and faunas through geological time was beginning to emerge. Charles Darwin, during the voyage of HMS *Beagle* in the early 1830s, became increasingly convinced that life was more diverse than he had imagined—every island he visited sported a new crop of plants and animals. He saw the lateral (geographic) and vertical (historic) links between species and realized by 1837 that species were all linked by a great tree. The tree concept made it clear why species that in his time were geographically close should also be genealogically close. Further, the tree concept made it clear why the fossil mammals he found in Argentina should be similar to the living mammals of the region.

This essay addresses four concepts: what we know about the sequence of the history of life, how life has diversified through time, how speciation occurs, and how good (or bad) the fossil record is as a source of data on the history of life. These were all issues that concerned Darwin (1859), and they concern us still today.

Narrative

There are many ways to recount the story of the history of life. As one of many typical examples, Benton and Harper (1997) presented a sequence of 10 stages from the origin of life to the origin of modern humans:

1. *The origin of life.* The appearance of the first evidences of life in the fossil record, some 3.5–3.6 billion years ago. These first, prokaryotic cells were probably like modern cyanobacteria ("blue-green algae"), but they lived in the absence of oxygen.
2. *Eukaryotes and the origin of sex.* The first eukaryote cells, with a nucleus, are reported from rocks dated about 1.3–1 billion years old and hence presumably appeared some time before that. The initiation of sexual reproduction, possibly at the same time as the origin of eukaryotes, possibly not, opened up the possibility of mixing of genetic material and recombination.
3. *Multicellularity.* The first multicelled fossils, red algae, are 1.26 billion–950 million years old, and this range of dates corresponds to molecular evidence that points to the origin of multicelled organisms some 1.2 billion years ago. Organisms consisting of many cells can diversify the functions of those cells, and they can become large.
4. *Skeletons.* Many animal groups apparently acquired hard, mineralized skeletons about 545 million years ago, at the beginning of the Phanerozoic, during the so-called Cambrian explosion. Animal fossils are known from many localities in the preceding Ediacaran, but the diversity of phyla represented by fossils expanded hugely when skeletons were acquired. The reasons for this are unknown, but skeletons clearly offered protection and support and permitted certain groups to enter new life zones.
5. *Predation.* Perhaps linked with the spread of skeletons, typically protective outer shells, may have been the rise of new kinds of predators, macroscopic animals such as trilobites that employed new strategies to feed on their large prey. Arms races between predators and prey became a standard feature of animal evolution thereafter.
6. *Biological reefs.* Reefs have existed since Cambrian times. They have been made from a broad range of animals; dominance shifted from polychaete worms in the Early Cambrian to archaeocyathans in the Late Cambrian and algae, bryozoans, stromatoporoids, and rugose and tabulate corals in the Ordovician, Silurian, and Devonian. Different groups of algae, sponges, bryozoans, and corals came and went through time, but reefs remained and are today dominated by scleractinian corals. Reefs are built from organisms, but they form major physical geographic features and provide a plethora of new habitats for life.
7. *Terrestrialization.* The move of life onto land similarly opened up a huge array of new life zones. Soils are known from some late

Precambrian successions, and soils imply life on land. Burrowing animals are known from Ordovician soils, while many small vascular plants and arthropods are known from the Silurian. Land plants became larger and more diverse in the Devonian, and the diversity of land-dwelling animals expanded to include worms, mollusks, many more arthropod groups, and vertebrates.

8. *Trees and forests.* Just as reefs in the sea are geographically substantial biological structures, so too are forests. The first trees in the Devonian were largely isolated, but massive forests developed in the Carboniferous, with trees up to 20 m tall. Not only did various land-plant groups diversify as trees, but other plants and animals that exploited the new habitats created by the trees also diversified.

9. *Flight.* A further expansion of ecospace was marked by the origin of flight. Insects arose in the Early Devonian, but the first true flyers were Carboniferous in age. Insects dominated the skies from then on. The first flying (gliding) vertebrates arose in the Permian and Triassic, while powered flight in vertebrates arose at least three times, in pterosaurs in the Late Triassic, in birds in the Late Jurassic, and in bats in the Tertiary.

10. *Consciousness.* The origin of consciousness in humans is much debated. Is this a feature of *Homo sapiens* alone, and hence present only in the past 200,000 years or so, or did earlier species of *Homo,* or even precursor genera such as *Australopithecus* and *Ardipithecus,* possess consciousness as much as 2 to 4 million years ago? Consciousness allowed humans to create things and to modify their environments and is the basis of the profound impact humans are having on the evolution of life.

These 10 stages are linked closely to major biological innovations (life, sex, multicellularity, skeletons, predation, consciousness) and major expansions in habitats occupied by life (reefs, terrestrialization, trees, flight). All 10 are documented to a greater or lesser extent in the fossil record.

In a more biologically oriented presentation, John Maynard Smith and Eörs Szathmáry (1995) identified eight major steps from the origin of life to human societies with language:

1. *Replicating molecules.* The first objects with the properties of multiplication, variation, and heredity were probably replicating molecules, similar to RNA but perhaps simpler and capable of replication but not informational because they did not specify other structures. A popular view is that RNA came before DNA because it can act both as a gene and an enzyme, views encapsulated in the term *RNA world.* If evolution were to proceed further, it was necessary that different kinds of replicating molecule should cooperate, each producing effects that helped the replication of others. For this to happen, populations of molecules had to be enclosed within some kind of membrane, or *compartment,* corresponding to a simple cell.

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2. *Independent replicators.* In existing organisms, replicating molecules, or *genes,* are linked together end to end to form *chromosomes* (a single chromosome per cell in most simple organisms). This has the effect that when one gene is replicated, all are. This coordinated replication prevents competition between genes within a compartment and forces cooperation on them, since if one fails, they all fail.

3. *RNA as gene and enzyme.* In modern organisms there is a division of labor between two classes of molecule: *nucleic acids* (DNA and RNA) that store and transmit information and *proteins* that catalyze chemical reactions and form much of the structure of the body (for example, muscle, tendon, hair). Perhaps originally RNA molecules performed both functions. The transition from an RNA world to a world of DNA and protein required the evolution of the genetic code, whereby base sequence determines protein structure.

4. *Eukaryotes and organelles. Prokaryotes* lack a nucleus and usually have a single circular chromosome. They include the bacteria and cyanobacteria (blue-green algae). *Eukaryotes* have a nucleus that contains rod-shaped chromosomes and usually other intracellular structures called *organelles,* including mitochondria and chloroplasts. The eukaryotes include all other cellular organisms, from the single-celled Amoeba and *Chlamydomonas* up to humans.

5. *Sexual reproduction.* In prokaryotes and in some eukaryotes, new individuals arise as *asexual clones* by the division of a single cell into two. In most eukaryotes, in contrast, this process of multiplication by cell division may be interrupted by a process of *sexual reproduction* in which a new individual arises by the fusion of two sex cells, or gametes, produced by different individuals.

6. *Differentiated cells.* Protists exist either as single cells or as colonies of cells of only one or a very few kinds, whereas *multicelled* organisms among animals, plants, and fungi are composed of many different kinds of cells, such as muscle cells, nerve cells, and epithelial cells. Each individual, therefore, carries not one copy of the genetic information (two in a diploid) but many millions of copies. The problem, of course, is that although all the cells contain the same information, they are very different in shape, composition, and function.

7. *Colonial living.* Most organisms are solitary, interacting with others of their species but not dependent on them. Other animals, notably ants, bees, wasps, and termites, live in *colonies* in which ouly a few individuals reproduce. Such a colony has been likened to a *superorganism,* analogous to a multicellular organism. The sterile workers are analogous to the body cells of an individual, and the reproducing individuals to the cells of the germ line. The origin of such colonies is important; it has been estimated that one-third of the animal biomass of the Amazon rain forest consists of ants and termites, and much the same is probably true of other habitats.

8. *Primate societies, human societies, and the origin of language.* The decisive step in the transition from ape to human society was probably the origin of language. In many ways human language is like the genetic code; information is stored and transmitted, with modification, down the generations. Communication holds societies together and allows humans to escape evolution.

Maynard Smith and Szathmáry (1995) argue that all but two of these eight transitions were unique, occurring just once in a single lineage. The two exceptions are the origins of multicellular organisms, which happened three times, and of colonial animals with sterile castes, which has happened many times. Had any of the other six transitions not happened, and that includes the origin of life itself (number 1), then we would not be here. That only two of the eight have demonstrably happened more than once speaks against Simon Conway Morris's (2003) thesis that convergence in nature is so prevalent that humanity and many other extant styles of life are virtually inevitable.

Diversification

NUMBERS

Life is astonishingly diverse today, with estimates ranging from 5 million to 100 million species, but perhaps, more soberly, homing in on a figure between 10 million and 15 million species (see the main essay "The Pattern and Process of Speciation" by Margaret B. Ptacek and Shala J. Hankison in this volume). Of these, fewer than 2 million have been recognized and described so far.

It is commonly assumed that life today is more diverse than it has ever been. This seems in some ways obvious, but it could also be construed as extraordinary vanity, somehow akin to the view that all evolution was planned to lead to human beings, and that somehow this instant in the vast span of time is the most important of all. However, it is evident that all living organisms and all organisms known as fossils derive from a single common ancestor (on the basis of the evidence of shared complex characters, such as the DNA-RNA system of inheritance, homeobox genes, and the like). That common ancestor, the single species that gave rise to all of life, existed some 3.5–3.8 billion years ago. But how many species have ever existed?

Biologists and paleontologists have tried a number of lines of reasoning to estimate the total number of species that have ever existed. Perhaps living biodiversity is only 2–4% of the total that has ever existed, as is suggested by three lines of reasoning (Sepkoski 1992; May 1994):

1. The first argument is based on an assumed pattern of species diversity increase and the known average duration of a species before it becomes extinct. If species diversity increased roughly linearly (additive model) through the Phanerozoic, and average species duration is 5–10 million

years, then living species represent 2–4% of those that existed during the past 600 million years.

2. The second argument is based on the diversification of insects over the past 450 million years. If the average duration of an insect species is 10 million years, and the group has diversified linearly, then 5% of all terrestrial species that ever existed are alive today.

3. The third argument is based on preservability of fossils. Some 250,000 species of fossil marine animals have been named, similar to the total number of known marine animal species alive today (200,000). Allowing for nonpreservation of soft-bodied organisms and other losses, this could also represent only 2–4% of the total number of fossil species (Sepkoski 1992).

In these discussions it has only been possible to examine patterns of diversification for macroscopic organisms, that is, typical plants and animals. Microbes are excluded because it has been hard to estimate their current diversity, and very little is known of their early fossil record. If 2–4% of all species that ever existed are alive today (10–15 million), there must have been some 250 to 750 million species in the past.

MODELS

Biodiversity, then, has expanded from one species to many millions of species today. But how? There are many ways to go from one species to many, and these can be expressed in terms of three mathematical models, represented by a straight line, an exponential curve, and a logistic curve, first as an uninterrupted increase (Figure 1A), and second with some mass extinctions superimposed (Figure 1B).

The *linear model* represents additive increase, the addition of a fixed number of new species in each unit of time. (The increase in this example and the others is a net increase, i.e., true increase minus extinctions.) In terms of an evolutionary branching model, additive increase would mean that through time speciation rates have declined, or extinction rates have increased regularly at a rate sufficient to mop up the excess speciations. The implied decline in the rate of evolution in the linear model comes about simply because the total number of species is increasing regularly, yet the *rate* of increase across the board remains fixed; hence, for any individual evolutionary line, the rate or probability of splitting (speciation) must decline. Such a model has generally been rejected as improbable.

The *exponential model* is more consistent with a branching mode of evolution. If speciation and extinction rates remain roughly constant, then there will be regular doubling of diversity within fixed units of time. A steady rate of evolution at the level of individual evolutionary lines scales up to an exponential rate of increase overall since total diversity is ever increasing. This model has been applied to the diversification rates of individual clades and to the diversification of life in general (Benton 1995; Hewzulla et al. 1999).
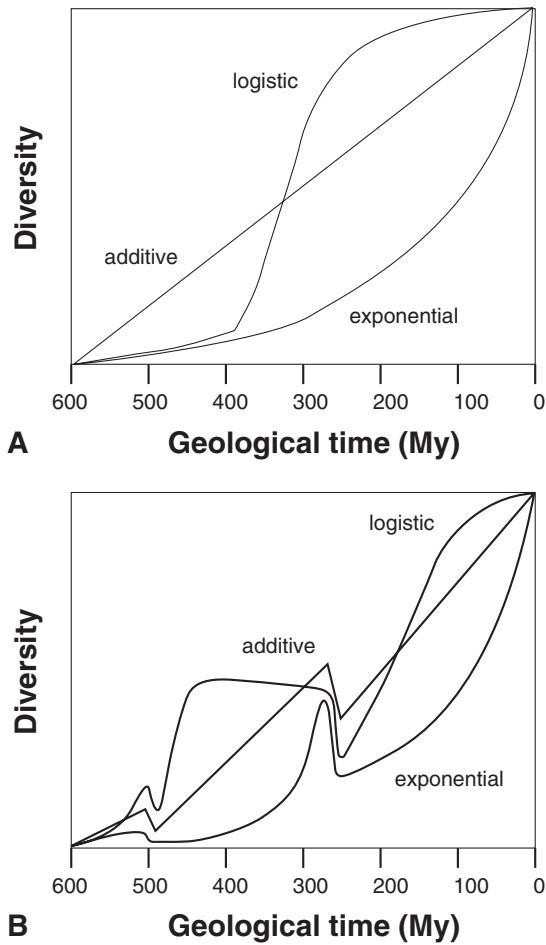
Figure 1. Theoretical models for the diversification of life plotted for the last 600 million years: (A) in the absence of major perturbation and (B) with two mass extinctions superimposed. In each case the upper curve is the logistic or equilibrium model, the middle curve is the additive or linear model, and the lower curve is the exponential model.

The *logistic model* involves one or more classic S-shaped curves, each consisting of an initial period of slow diversity increase, a rapid rise, a slowing of the rate of increase as a result of diversity-dependent damping factors, and then a plateau corresponding to a limiting or equilibrium value. The logistic model has been used to explain patterns of diversification of marine organisms (Sepkoski 1984) and of plants (Niklas et al. 1983).

There is clearly no consensus on which model best explains the diversification of major sectors of life through time, or on whether all patterns of diversification adhere to the same model of increase. The choice of model is important since each makes profoundly different claims about evolution.

LAND AND SEA COMPARED

There are major differences between the patterns of diversification on land and in the sea, and the history of life in each realm may have been rather different. Today about 85% of described species of plants and animals live on land, and the main groups (plants, arthropods, vertebrates) have reached their present great diversity in the past 450 million years. Plants and animals have been evolving in the sea since at least 600 million years ago, and the fossil record is dominated by marine species, which make up some 95% of all described forms. This dominance of marine organisms is partly accounted for by the facts that virtually the only organisms known from the Vendian and early Paleozoic (600–450 million years ago) are marine, and that the early history of life on land appears to have occurred at relatively low diversities. Also, fossils in certain marine environments are more likely to be preserved than those in many continental settings. The observation that life on land today is apparently five to six times as diverse as life in the sea, largely because of the insects, could be an artifact that reflects the greater amount of time devoted by systematists to continental than to marine organisms. However, if this difference is even partly correct, then it would imply a much more rapid diversification on land than in the sea.

In studies of the diversification of marine animal families (Figure 2A), there is evidence for a short plateau in the Cambrian (lasting about 40 million years) and a longer one from the Ordovician to the Permian (about 250 million years). This is followed by a long phase (250 million years) of near-exponential increase in diversity through the Mesozoic and Cenozoic, the rising element of a third logistic curve, which shows a hint of a slowdown in the last 25 million years or so, suggesting that a third plateau level may be achieved 125 million years in the future (Sepkoski 1984).

Marine invertebrate diversification has been explained (Sepkoski 1984) as the succession of three major phases of evolution, in which broad assemblages of different phyla *(evolutionary faunas)* dominated the oceans and were then replaced. The Cambrian fauna diversified exponentially at first, and then diversification slowed as the equilibrium level of 85 families was approached. The exponential diversification of the Paleozoic fauna then began in the early Ordovician, reaching an equilibrium diversity of 350 families and largely supplanting the Cambrian fauna. Finally, after the mass extinction at the end of the Permian, which reduced the global diversity of the Paleozoic fauna dramatically, the Modern fauna continued and accelerated its long-term rise in diversity.

In studies of the diversification of vascular plants (Figure 2B), an equilibrium interpretation has also been given (Niklas et al. 1983). There was a succession of major *Baupläne* (ground plans or archetypes) of plant types: early vascular plants in the Devonian; lycopods, ferns, conifers, and others in the Carboniferous to the Permian; gymnosperms in the Triassic to the Jurassic; and angiosperms from the Cretaceous onward. There is evidence for declining speciation rates and increasing species durations during each of the first
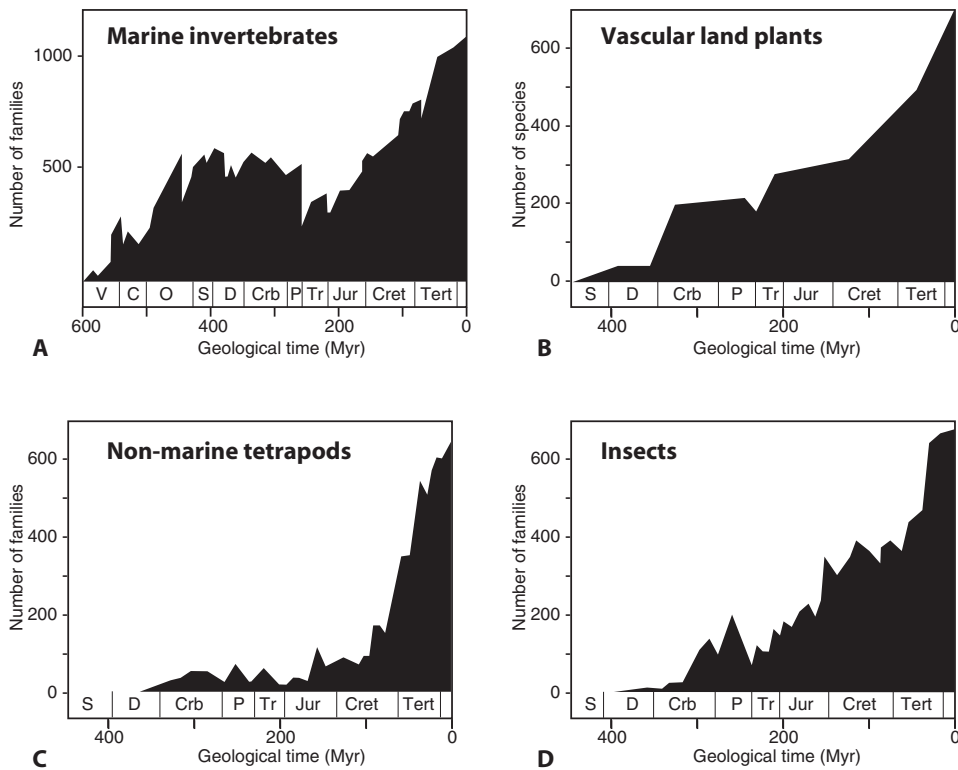
Figure 2. Patterns of diversification of families of marine invertebrates (A), vascular land plants (B), nonmarine tetrapods (C), and insects (D). Stratigraphic abbreviations: C, Cambrian; Crb, Carboniferous; Cret, Cretaceous; D, Devonian; Jur, Jurassic; O, Ordovician; P, Permian; S, Silurian; Tert, Tertiary; Tr, Triassic; V, Vendian. (Based on Sepkoski 1984; Niklas et al. 1983; Benton 1985; and Labandeira and Sepkoski 1993.)

three radiations as the new set of clades partially replaced the old. Each new radiation led to an increase in total global diversity, while the diversity of the preceding floras declined. Angiosperms apparently continued to diversify at a high rate. It is hard to identify plateaus in land-plant species diversification, and it is hard to find evidence for logistic models of diversification. Equally, the total curve of species diversities through time is not obviously exponential, and, if anything, the pattern appears to suggest linear increase in diversity through time.

The diversification of continental tetrapod families (Figure 2C) appears to correspond to an exponential model of increase (Benton 1985). Diversity levels remained low, at some 30 to 40 families, during the late Paleozoic and much of the Mesozoic. They then rose to about 100 families at the end of the Cretaceous and, after recovery from the end-Cretaceous extinction event, familial diversity increased rapidly toward 330 families and shows no sign of a slowdown. The pattern of diversification may be dissected into successive radiations of three global clade associations: basal tetrapods (formerly termed

labyrinthodont amphibians) and synapsids (mammal-like reptiles) in the late Paleozoic; archosaurs (dinosaurs, pterosaurs, crocodilians) in the Mesozoic; and lissamphibians (frogs and salamanders), lepidosaurs (lizards and snakes), birds, and mammals from the late Cretaceous to the present day. These clade associations replace each other and are associated with ever higher global familial diversity levels, but it is difficult to fit logistic curves to any of the associations.

The diversification of insects (Figure 2D) was also apparently exponential, especially in the Mesozoic portion of the curve (Labandeira and Sepkoski 1993). This suggests that insects have had a long and continuous pattern of expansion that perhaps slowed somewhat during the Tertiary. This may indicate that insect diversity is approaching an equilibrium level now.

Plots of the diversification of families of marine, continental, and "all" life (Figure 3) by Benton (1995) confirm these varying models of diversification. The continental curve (Figure 3B), dominated by tetrapods, insects, and land plants, is exponential. The marine curve (Figure 3C) retains a Paleozoic plateau level and appears to show a slowdown in diversification towards the Recent, which may indicate that marine diversity levels today are approaching an equilibrium level. The curve that combines all marine and continental families (Figure 3A) could be interpreted as a single poorly fitting exponential curve (Hewzulla et al. 1999), but the Paleozoic plateau, reflecting the contribution of marine invertebrates (compare Figure 3C), cannot be ignored.

EXPLANATIONS OF PATTERNS OF DIVERSIFICATION

In comparing logistic and exponential models for the diversification of life, the key distinction is between equilibrium and nonequilibrium (or expansion) models. The former imply the existence of global equilibria in diversity, while expansion models assume that there is no ceiling to the diversity of life, or at least that such a ceiling has yet to be reached.

Equilibrium models for the expansion of the diversity of life were based on an influential body of ecological theory. Logistic modeling of global-scale data on diversification assumes (1) interactions among species within clades, (2) interactions between clades, and (3) global equilibrium levels. Many studies show that clades may radiate initially at exponential rates, but that the rate of diversification slows at a certain point as a result of diversity-dependent phenomena, such as competitive exclusion, increased species packing, and reduction of species ranges (Sepkoski 1984, 1996). This style of reasoning follows explicitly from classical experiments in competition where the increase of one population suppresses another that depends on the same limiting resource. An initial exponential increase of the successful population is followed by a plateau when the species begins to deplete the limiting resource (usually food); this corresponds to the local carrying capacity.

The pattern of diversification of marine families (Figure 2A) has been interpreted (Sepkoski 1984, 1996) in terms of a three-phase logistic model that

A All Organisms

B Continental Organisms

C Marine Organisms
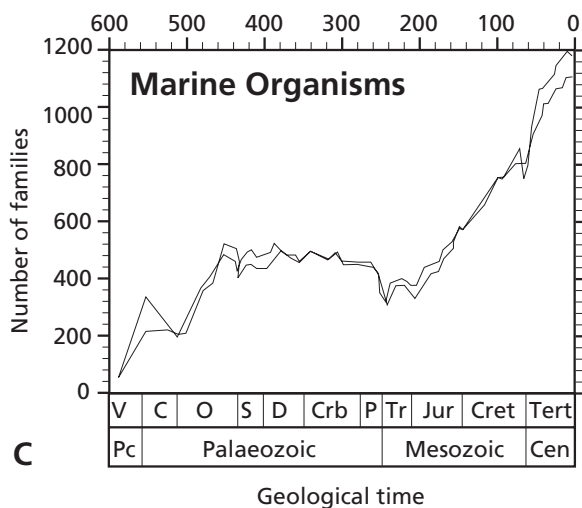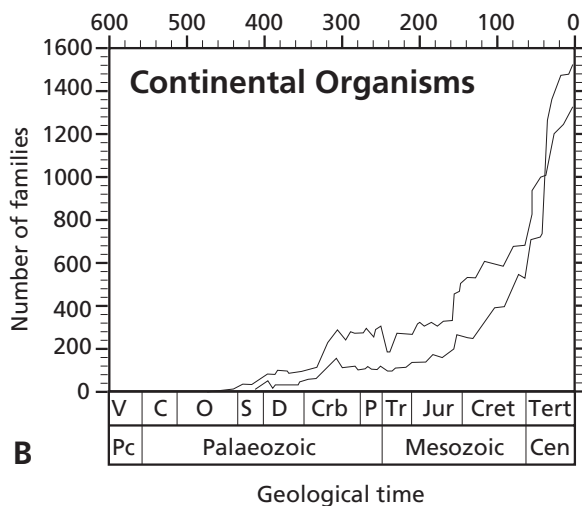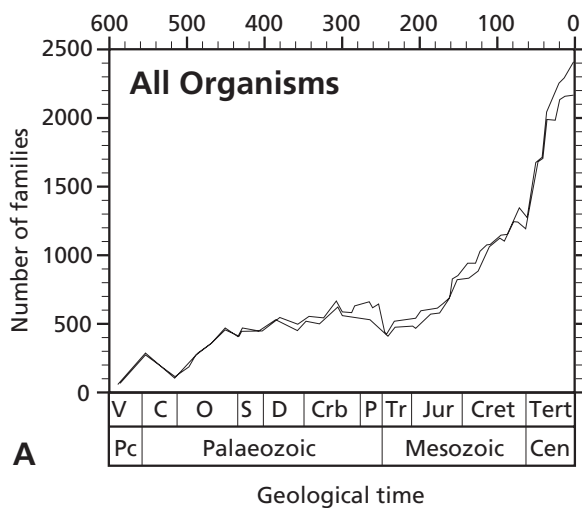
represents the behavior of the three evolutionary faunas: Cambrian, Paleozoic, and Modern. The replacing faunas are said to have been characterized by the ability to penetrate ever wider sets of niches and hence to achieve higher diversities. There is some evidence in favor of this idea; for example, later marine animals could burrow deeper, form more complex reefs, and capture prey in ever more ingenious ways. The equilibrium models could be interpreted simply in terms of large-scale competition between major clades, with bivalves outcompeting brachiopods, mammals outcompeting dinosaurs, and so on. Despite the popular appeal of such suggestions, most supposed cases of large-scale competition crumble when the evidence is examined (e.g., Gould and Calloway 1980; Benton 1987). Sepkoski (1996) attributed the patterns of waxing and waning of clades to diffuse competition between them at the species level, where species in one clade are generally competitively superior to those in another. However, there are four areas of concern with equilibrium models:

1. There is no independent evidence for equilibria, that is, for fixed carrying capacities on the earth today. In evolutionary terms equilibrium diversities imply that all available resources are in use and all ecospace is filled. If a new species originates, it must displace a preexisting one. However, observations of cases where previously isolated floras and faunas come into contact suggest that species are just as likely to insinuate (enter new niches) and not cause extinction of other taxa.

2. Multiple logistic models imply predictable outcomes of interactions between members of the different faunas, that is, that members of one group will generally succeed where those of another will fail. Where major biotic replacements have been investigated, one group is more likely to disappear because of an extinction event (Benton 1987) than as a result of interactions.

Figure 3. Patterns of the diversification of life through time in terms of changes in numbers of families extant per stratigraphic stage, plotted for all organisms (A), continental organisms (B), and marine organisms (C). In each graph a maximum and a minimum are shown, based on a combination of stratigraphic and habitat-preference information. The minimum measure includes only families recorded as definitely present within each stratigraphic stage or as definitely spanning that stage, and only families designated as restricted solely to the marine or continental realm. The maximum measure includes also all doubtful stratigraphic attributions of families and all equivocal and shared habitat designations. The sum of minimum measures for continental and marine organisms is equal to the minimum measure for all taxa together. The sum of maximum measures, however, does not equal the maximum measure for all taxa because families with equivocal environmental assignments and those that occur in both marine and continental settings are counted as both marine and continental. Stratigraphic abbreviations as in Figure 2 with the addition of Cen, Cenozoic; Pc, Precambrian. (Based on Benton 1995.)

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3. The diversification of the Modern fauna seems more prolonged and
   slower than predicted by a logistic model. The rising phase of the
   logistic curve has lasted for 250 million years, with some evidence of a
   slowdown toward the present. If there is no current plateau, then it
   would seem that in the second half of the Phanerozoic, the best-known
   part of the fossil record, the logistic rules have been forgotten.

4. The classic logistic curves of Sepkoski (1984, 1996) may be artifacts of
   the level of analysis. The curves are plotted at the level of families.
   When these are translated to the generic level, the logistic patterns
   begin to break down, and at species level the pattern could be
   exponential (Benton 1997). The shape of the curves switches because
   each genus contains many species, and each family many genera. In an
   evolutionary tree the species are the final twigs, while genera extend
   deeper into the tree, and families deeper still. So, although the number
   of families might be defined at a constant level, the number of species
   in each could be expanding exponentially.

The alternative to equilibrium is *expansion.* Are the aggregate patterns, or
at least some of them (Figures 2 and 3), the result of unconstrained expan-
sion? Certainly, some clades (such as insects, angiosperms, birds, and mam-
mals) seem to continue radiating linearly or exponentially for many tens or
hundreds of millions of years. Such ever-expanding patterns imply that
these groups are highly successful and adaptable. The overall patterns of
diversification (Figure 3) incorporate the numerous constituent clades, some
expanding, others diminishing, and others remaining at constant diversity at
any particular time. From an expansionist viewpoint, there is no prediction
of how the individual clades affect each other. New global diversity levels
may be achieved by combinations of new adaptations, habitat changes, and
extinction events. In the past 250 million years the diversification of life has
been dominated by the spectacular radiations of certain clades both in the sea
(decapods, gastropods, teleost fishes) and on land (insects, arachnids, an-
giosperms, birds, mammals). There is little evidence that these major clades
have run out of steam and nothing to indicate that they will not continue to
expand into new ecospaces.

Exponential increase could imply that diversification would last forever.
Presumably there is a limit to the numbers of families or other taxa that can
inhabit the earth at any time: such a limit would be caused not least by the
amount of standing room on the ark. If a limit of living space were ap-
proached, ever smaller organisms would presumably be favored by selection.
Equally, as has happened many times during evolution, organisms would
take unexpected measures to survive, for example, by occupying the air, bur-
rowing into sediments, and, in the case of some bacteria, living deep within
the earth's crust. With size reduction, the ultimate limit to the diversification
of life might then become the availability of the chemical components of life,
principally carbon.

EQUILIBRIUM OR EXPANSION?

It is hard to select between the two models for the diversification of life. Until recently, equilibrium models have dominated the thoughts of paleobiologists, just as they have dominated the minds of ecologists. However, just as ecologists are now questioning the oversimplistic equilibrium models they accepted in the 1960s and 1970s, so paleobiologists are reconsidering how diversification might have happened in the longer term.

The equilibrium model assumes that specific major ecological realms can accommodate only certain numbers of species, and that when the carrying capacity is reached, net diversification ceases. The expansion model makes no such assumption and allows for continuing, if episodic, diversification with no ultimate limit in sight.

Paleobiologists have debated and continue to debate which model is correct. Perhaps all life has diversified according to either an equilibrium or an expansion model. Or perhaps different sectors of life diversified in different ways. Evolution in the sea may have resulted in a greater level of stability, and patterns of increase may have generally been logistic, while life on land may have diversified exponentially since the first plants and arthropods crept cautiously out of the water. The implications of the equilibrium and expansion models are profoundly different, not merely for paleobiologists, but for everyone concerned about the present and future state of global biodiversity.

Speciation

The effort to understand how life diversified from its origin to the present day is at the upper end of the spectrum of studies in *macroevolution.* At the lower end the important crossover between paleobiology and modern evolutionary studies is *speciation* (see the main essay "The Pattern and Process of Speciation" by Margaret B. Ptacek and Shala J. Hankison in this volume), the formation of new species by the splitting of *lineages* (evolutionary lines).

Paleobiologists clearly cannot use the *biological species concept* since they cannot test whether any two fossil specimens are capable of interbreeding, so they seek to apply the *morphological species concept,* in which species are distinguished by differences in their phenotypes. This may at first seem to be a weak substitute, but there are shared assumptions: paleobiologists use populational thinking, seek to characterize species boundaries on the basis of statistical studies of large samples of specimens, and assume that speciation involves morphological differentiation associated with reproductive isolation. In practice, this is not very different from the approach of many systematists of modern organisms—species of mollusks are generally determined from morphology, and fossil and extant material may form parts of a seamless study. Systematists rarely carry out interbreeding trials.

Until 1970 most evolutionists assumed that fossils could say very little original about speciation. Then Eldredge and Gould (1972) challenged the consensus with their theory of evolution by punctuated equilibria. Eldredge and Gould termed the standard viewpoint *phyletic gradualism*. It assumed that evolving lineages were changing at variable rates (Figure 4A) but were changing more or less continuously *(anagenesis)*. Speciation was seen as a by-product of this process of change: sometimes lineages had become so different from their starting points that they had evolved into a new species (the *chronospecies* concept). Speciation by splitting *(cladogenesis)* could also happen, but the process was no slower or faster than normal rates of lineage evolution.

The opposing viewpoint, evolution by *punctuated equilibria* (Figure 4B), proposed that rapid morphological change at cladogenesis, rather than anagenesis, was the most important process. The normal state of a lineage was *stasis* (no change), and from time to time speciation would happen, but such speciation events were rapid and revolutionary. The punctuated-equilibrium model makes two claims: that rates of change along a lineage are punctuated, and that rapid change is correlated with speciation events. The latter claim was the most controversial, but it has been regarded as the key, defining element of the punctuated-equilibrium model by its supporters.

Eldredge and Gould based their new model on two observations:

1. Stasis is common in the fossil record. Fossils can remain constant in appearance through many meters of sediment (i.e., thousands or millions of years), and then everything seems to change.
2. If most speciation happens according to Mayr's *allopatric* (geographic-splitting) model, then it would appear as a rapid event in the fossil record. The detail of the gradual divergence of two isolated populations would not be seen.
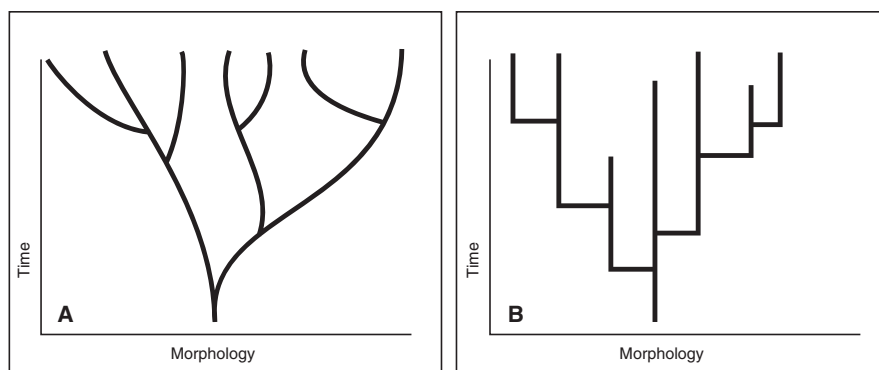

Figure 4. Contrasting expectations of species-level evolution in the classic phyletic-gradualism model (A) and the punctuated-equilibrium model (B). Degree of morphological change is indicated on the x-axis, time on the y-axis.

The punctuated-equilibrium versus phyletic-gradualism debate of the 1970s and 1980s was huge fun for all concerned, not least because the protagonists kept shifting ground and revising their claims. The first phase was based on the ideas in Eldredge and Gould's essays. From 1975 onward several supporters of punctuated equilibria extended the model to espouse a new idea of *species selection,* a higher-order process in which species were sorted and, in some models, could even undergo selection of "emergent" higher-order characters. Species selection could, in theory, occur independent of, and even in opposition to, natural selection (Stanley 1975). This led to the idea of an "expansion" of evolutionary theory to many hierarchical levels (Gould 1990), with hints of an apparent rejection of aspects of the neo-Darwinian view. Such extreme positions were abandoned fairly rapidly by most enthusiasts, and paleobiologists continued their staunch adherence to natural selection during the late 1980s and 1990s. Species selection is generally considered to be theoretically possible but extremely feeble and unlikely to result in significant adaptations of the type that occur in the natural selection of individuals. However, the notion of stasis stuck: too much fossil evidence pointed to its importance, and quantitative genetic models were found to explain it (Lande 1986).

A plethora of case studies was assembled and published from 1975 to 1990 that purported to test the phyletic-gradualism versus punctuated-equilibrium views. Early efforts were often inadequately documented and did not provide enough evidence about the accuracy of dating and the possibility of migrations of taxa in and out of the study area. It soon became clear that what was a gradual anagenetic pattern to one person was an obviously stepped, punctuational pattern to another. Some studies (e.g., Williamson 1981; Sheldon 1987) involved hundreds of thousands of specimens and an intense focus on fine-scale dating and statistical analysis of huge samples, but they were still subject to criticism. For example, Sheldon's (1987) study of trilobites showed a great deal of anagenesis and stasis, but his sampled lineages just did not speciate. Williamson (1981) believed that he had documented a number of punctuational speciation events, but they were generally interpreted as more likely to be examples of *ecophenotypic* change, that is, nongenetic change in shape resulting from temporary environmental stresses.

The fossil record demonstrates the widespread occurrence of stasis. Erwin and Anstey (1995) summarized the results of 58 studies of speciation patterns in the fossil record published between 1972 and 1995. Organisms ranged from radiolaria and foraminifera to ammonites and mammals, and stratigraphic ages ranged from the Cambrian to the Neogene, with the majority concentrating in the Neogene, the past 25 million years of the history of the earth. Of the 58 studies, 41 (71%) showed stasis, associated either with anagenesis (15 cases; 37%) or with punctuated patterns (26 cases; 63%). It seems clear, then, that stasis is common in species-level evolution, and it had not been predicted from modern genetic studies.

What then of the punctuated-equilibrium versus phyletic-gradualism debate? As ever, the protagonists on either side sought to demonstrate the

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ubiquity of their model, and yet common sense suggests that there are clear biological reasons that each model prevails under particular circumstances. Benton and Pearson (2001) noted that speciation is a consequence of reproductive isolation, and hence the frequency of speciation in a group is likely to be related to the ease with which reproductive barriers appear. At one extreme there are organisms such as planktonic protists that live in huge populations that seldom encounter barriers to dispersal, and that do not possess complex behaviors associated with reproduction. For these, genetic isolation of populations is a rare event, and speciation, which perhaps occurs rarely, is probably generally long term and gradual, lasting perhaps half a million years. At the other extreme are organisms such as freshwater fishes that live in spatially structured and often-transient environments. Here speciation might be so common that every lake and river has its own reproductively isolated population of a particular type of fish, but these populations might neither be very distinctive nor last very long. In between might lie the majority of invertebrate and vertebrate groups, generally exhibiting stasis but from time to time speciating in a punctuational way as a result of a major perturbation in the environment.

A fine example of speciation in a marine protist is seen in *Rhizosolenia,* a planktonic diatom that occurs today in huge abundance in the equatorial Pacific (Sorhannus et al. 1998). The siliceous valves of this genus have accumulated for millions of years on the seabed, and they have been sampled back to 3.4 million years ago from cores. Huge samples of the valves can be taken every few millimetres through the sediment pile, and these can be dated accurately. Today there are two species of *Rhizosolenia* living side by side in the oceans, *R. bergonii* and *R. praebergonii,* and these can be tracked back for some 2.6 million years. Then, from 2.6 to 3.1 million years ago, the morphologies of the two species converge and fuse, and there is apparently only a single lineage before that time (Figure 5). This splitting event is reported from eight different seabed cores, and the morphological divergence occurs in several morphological characters, so it was evidently not a local event but occurred throughout the equatorial Pacific. Diatoms generally reproduce asexually, but they occasionally produce sexual offspring. Perhaps the combination of a generally asexual reproductive mode and the barrierless Pacific Ocean explains why *Rhizosolenia* speciated phyletically and over a span of some 400,000 to 500,000 years.

It seems probable that sexually reproducing animals that live in varied habitats more often show punctuational speciation. *Metrarabdotos* is an ascophoran cheilostome bryozoan that is represented today in the Caribbean by three species. Coastal rocks of the Dominican Republic and elsewhere in the Caribbean document the past 10 million years of sedimentation in shallow seas, and they yield abundant fossils of this bryozoan. The fossils show that *Metrarabdotos* radiated dramatically from 8 to 4 million years ago, splitting into some 12 species, most of which had died out by the Quaternary (Figure 6). Studies by Cheetham and Jackson (1995) have established a variety of protocols for distinguishing species within *Metrarabdotos,* taking into
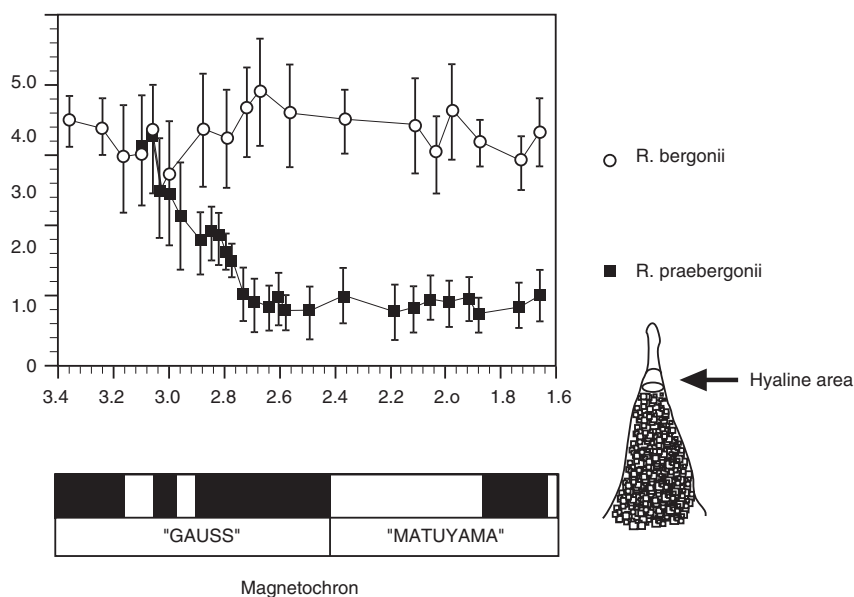
**Rhizosolenia
(planktonic diatom)**

Figure 5. Gradual speciation in the diatom *Rhizosolenia.* One of several morphological characters, the height of the hyaline area, that differentiate the two living species *R. bergonii* and *R. praebergonii.* This plot, from one of eight sampling stations on the floor of the Pacific Ocean, shows a long-term divergence between the two species from 3.1 to 2.6 million years ago, as the populations slowly differentiated. The sedimentary record is continuous, and it can be dated by fossils and by magnetic reversal measurements, indicated in the magnetochron scale at the bottom.

account the genetics and the amount of morphological differentiation of related extant species and then extending comparable statistical tests of morphological differentiation to the fossil forms. Lineage splitting in *Metrarabdotos* seems to have been rapid and punctuational in character. Speciation was especially rapid from 8 to 7 million years ago, with nine new species appearing in that time, although sampling may be a problem in rocks of this age. However, the interval from 8 to 4 million years ago, represented largely by information from Dominica, has been intensely sampled. So, although there are questions over the origins of the nine basal species within this interval, the origins of the remainder (*tenue,* new species 10, and new species 8) are more confidently documented as being punctuational.

The plurality of evolutionary modes (gradualism without stasis, gradualism plus stasis, punctuation plus stasis) might be real, and there might be environmental controls that work in a somewhat unexpected way. Sheldon (1996) proposed that gradualism might characterize taxa that live in stable environments and change in line with slow environmental changes, whereas
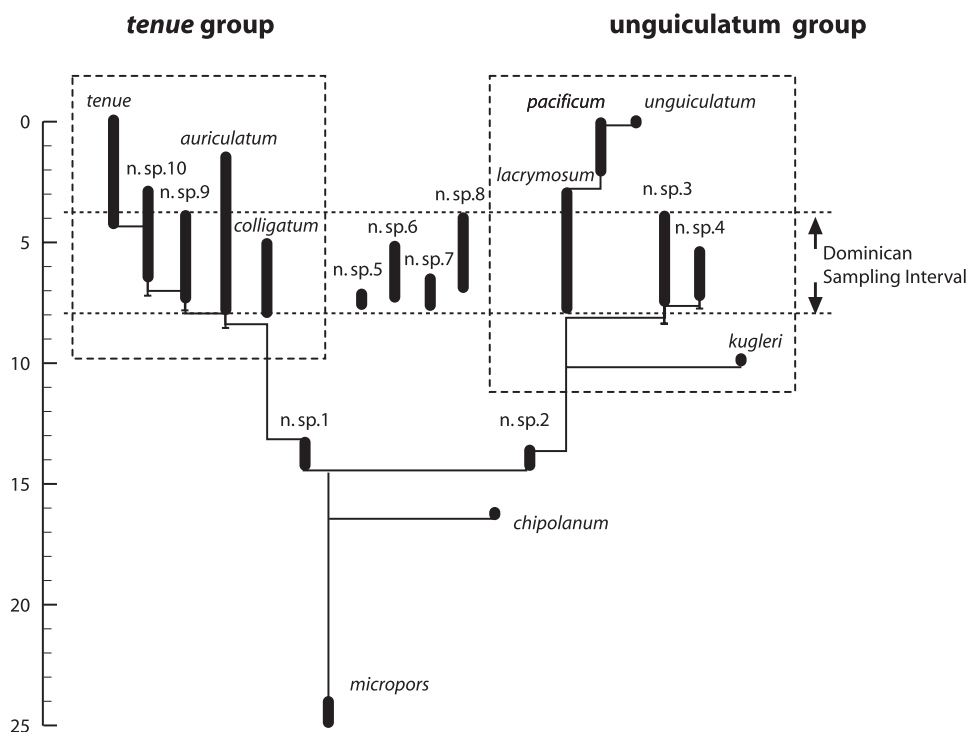
Figure 6. Punctuational speciation in the bryozoan *Metrarabdotos*. The three living species are documented by fossils, but a further nine species are extinct. Intense collecting throughout the Caribbean has revealed the pattern of speciation. Sampling in the time from 25 to 8 million years ago is sporadic, but the time from 8 to 4 million years ago, the Dominican Sampling Interval (DSI), is extremely well known, based on a fine and continuous fossil record on the island of Dominica. Species distinctions are based on a combination of morphological and genetic studies. (Image courtesy of Alan Cheetham.)

stasis might be a feature of taxa that occupy unstable environments, which can vary rapidly and dramatically, but those taxa do not evolve in line with every environmental fluctuation.

Quality

The quality of the fossil record has obsessed and continues to obsess paleobiologists. Ever since Darwin (1859, 279) considered the "imperfection of the geological record," paleobiologists and others have oscillated in their confidence. Some have claimed, perhaps rather wildly, that everything the fossil record says is correct, while others, perhaps equally wildly, have rejected the fossil record as being next to useless. The truth presumably lies somewhere between, and most people tacitly veer to the positive end of the spectrum. A number of major challenges have arisen recently, however, and I shall touch on these briefly.

A qualitative argument first, in favor of the fossil record, is that since 1859 nothing much new has come to light. In the historical context, Charles Lyell was still in 1859 arguing for nonprogression, that he might expect to find Silurian reptiles and Devonian mammals, and that ichthyosaurs might one day return to earth. Darwin argued for progression of life forms through time, of course, and he knew about trilobites in the Silurian, armored fishes in the Devonian, amphibians in the Carboniferous, reptiles in the Permian, dinosaurs in the Triassic, and mammals and birds in the Jurassic. In the 150 years since 1859, and despite the input of millions of hours of searching, paleontologists have simply adjusted the mid-Victorian picture: the origin of agnathan fishes has been pushed back from the Silurian to the Cambrian, the origin of amphibians from the early Carboniferous to the latest Devonian, the origin of reptiles from the early Permian to the mid-Carboniferous, and the origin of mammals from the mid-Jurassic to the late Triassic. The origin of birds has remained unchanged in the latest Jurassic. Were the fossil record hopelessly unrepresentative, new finds should provide major surprises from time to time.

The notion of a good fossil record was confirmed in quantitative analyses by Maxwell and Benton (1990) of the vertebrate record and Sepkoski (1993) of the marine animal record. The first authors looked at the accumulation of knowledge from 1890 to 1987, the second at changes from 1982 to 1992. In both cases the sum totals of diversity through time increased, essentially doubling in 100 years, but the increases were randomly distributed with respect to time, and so the overall patterns of diversifications and extinctions remained unaffected. In a further study Benton and Storrs (1994) tested whether new fossil discoveries tend to fill predicted gaps or create new gaps. They found the former: in 25 years of study, new fossil finds had improved the completeness of the tetrapod fossil record by some 5% by plugging gaps more often than creating new gaps.

There have been two major challenges to this somewhat complacent view: sampling effects and molecular phylogenies. In both cases the critics accept that the fossil record as documented is well understood. However, they highlight the fact that the fossil record itself is a poor sample of life. So, however well known it is, the fossil record can never document the evolution of soft-bodied organisms adequately, and other groups—perhaps microscopic, perhaps living in unusual environments—may similarly not be fossilizable.

The criticisms of sampling, although linked, have had different foci. Smith (2001, 2007) argued that the fossil record is closely tied to the sedimentary rock record, which itself is linked to sea-level changes, and that many supposed extinction events are nothing more than changes of environment. If there is a major regression (retreat of the sea), shallow marine organisms apparently disappear from sections. This could be recorded as an extinction, but it is merely a sedimentary artifact. Smith (2001, 2007) pointed out, however, that the diversification of life in the sea during the last 250 million years is probably real because sea levels were falling during this time: the rise in diversity is not driven by a rise in sea level.

Peters and Foote (2001, 2002) went one step further, arguing that virtually all the fossil record is closely dependent on the sedimentary record. Supposed extinctions, diversifications, and other biological patterns are all apparently driven by the volume of preserved rock. These authors found that the diversity of life apparently matches the number of named rock formations in North America. So, they argued, when life appears to be diversifying, it is simply because there is more sedimentary rock and hence more fossils. When a mass extinction is identified, it is nothing more than a loss of appropriate rocks in which to preserve fossils.

These views have been seen as perhaps rather extreme (Benton 2003; Peters 2005). The correlation of numbers of named formations and diversity of life reported by Peters and Foote (2001, 2002) could be reversed: it is just as likely that when life is diverse and fossils are abundant, geologists recognize and name more formations. In general, of course, as we always teach our students, correlation does not imply causation. Further, assuming that rock volume, or some proxy for rock volume, is pure error in our understanding of the fossil record and should then be applied as a correction factor is heavy handed—major biological events such as diversifications and mass extinctions are removed at a stroke. As Peters (2005) pointed out, there is no reason to reject the proposal that marine rock volume and marine diversity might vary in concert with a third factor, such as sea-level change. Abundant marine rocks and abundant marine fossils might actually reflect high sea levels and abundant marine life: in such a case, to divide the peak in marine diversity by the peak in marine rock volume would effectively remove that (true) biological signal. Much more work is required to investigate further why the marine rock and fossil records are correlated, but the terrestrial rock and fossil record appears not to be (Fara 2002).

The second major current challenge to the informativeness of the fossil record comes from molecular studies and debates about the timing of origins of major groups. Some molecular estimates place the origins of Metazoa (animal phyla), green plants, angiosperms, and modern orders of birds and mammals at points up to twice as old as the oldest representative fossils (e.g., Wray et al. 1996; Cooper and Penny 1997; Kumar and Hedges 1998; Wray 2001; Hedges and Kumar 2004). The range of molecular estimates for the origin of metazoans is 0.6 to 1.2 billion years ago, with most estimates closer to 1 billion years ago than 600 million years ago. The range of molecular estimates for the origin and basal splitting of placental mammals and modern birds is 130 to 70 million years ago, again with more estimates nearer 120 million than 70 million. The first fossils date, respectively, from around 600 and 70 million years ago.

The mismatch of first fossil dates and first molecular dates could indicate major errors in one or the other source of data or both. Many commentators (e.g., Easteal 1999; Wray 2001; Hedges and Kumar 2004) have argued that the fossil dates are almost certainly wrong, and that the molecular dates are closer to the truth. Others (e.g., Benton 1999; Bromham and Hendy 2000; Benton and Ayala 2003) have suggested potential problems with both

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approaches: fossil dates are always too young, of course (one never finds the first fossil of a group), but not outrageously too young, while the molecular dates tend to be too old, sometimes by a long way. Graur and Martin (2004), speaking from the molecular side, present a robust attack on the evidence for molecular age doubling just noted, while Hedges and Kumar (2004) defend their position. On balance, however, the molecular findings that seemed like a devastating exposure of the frailties of the fossil record in 1996 have now been shown to rest on far weaker ground than was first asserted.

Do these debates just reduce to assertion and counterassertion? Can we ever bridge the gap between knowledge of the fossil record (which is accepted to be good) and the problem of unpreserved life of the past? Perhaps this can be done to some extent. In a brilliant example of lateral thinking, Norell and Novacek (1992) realized that evolutionists uniquely had three independent sources of data on the history of life: fossils, cladistics, and molecular phylogeny. By fossils they meant the stratigraphic order of occurrence of fossils in the rocks. Cladistics and molecular phylogeny reconstruction are relatively new approaches to drawing evolutionary trees, whether on the basis of morphological or molecular characters, and they are independent of stratigraphy. Norell and Novacek (1992) proposed that all three approaches could be compared for congruence (agreement). Up to that point no one knew whether the fossils or the trees were in any way close to the truth: without a time machine, or omniscience, how could one tell? They argued, though, that if the fossil sequences and the sequences of branching points in the trees were congruent, then probably the fossil record did represent the true pattern of the history of life. Lack of congruence could indicate that either the fossil record is wrong or the trees are wrong, or both. Studies can be done group by group, and they show good congruence in as many as 75% of cases (Norell and Novacek 1992; Benton and Storrs 1994; Benton et al. 2000). These studies indicate that all groups examined are about equally well preserved in the fossil record, that there is no substantial difference between marine and continental fossil records, and that there is no time bias (for broad-scale phylogenetic trees plotted against stage-level divisions of time).

Conclusion

Paleontology is an ancient subject, dating back to the sixteenth or seventeenth centuries. To many, it had its heyday in Victorian times, and little has happened since beyond the discoveries of new dinosaurs and hominids reported weekly in *Science* and *Nature*. In a sense, as I have argued, that is true, and the fact that (despite the claims) these new discoveries are rarely shocking is strong evidence that the fossil record tells us something truthful about the history of life.

But the history of life is more than just a narrative of first one fossil, then another, group A giving way to group B, and so on through to mankind. The narrative is important for what it tells us about the astonishing inventiveness

of life, its ability to evolve and do unpredictable things. Which Devonian ob-server would have predicted that the multilimbed insects that crept round the waterside plants would one day take to the air? Which Jurassic observer would have guessed that the insects she saw flitting and dancing in the sun-light around the muddy legs of the dinosaurs would evolve sociality and then drive their biodiversity and global biomass to untold levels? Current biodiver-sity is higher than it ever has been. Where might life evolve next? There are in-timations of microbes that live in ice and in boiling waters, and some that live perhaps three kilometers down within the rocks beneath the sea floor. These examples strain credulity, but they have happened and are happening.

There is more to the study of the history of life, though, than mere docu-mentation of fossils. Fossils represent extinct groups. Dinosaurs cannot be predicted from molecules, but they existed and show us organisms that did what no living animal does. Some dinosaurs were 10 times the mass of the largest living mammals. Some pterosaurs had wingspans three or four times those of the largest birds today. Some extinct arthropods were larger than any alive today. These organisms are all truly wonderful, and they pose in-teresting problems for biomechanicists and physiologists.

Diversifications and mass extinctions can be predicted (retrodicted?) from studies of modern phylogenies, but the details have always remained mysteri-ous. Paleontologists have the great pleasure of being able to dissect such events in fine detail, and as fossil-collecting techniques, the precision of dat-ing, and environmental analytical tools improve, the level of understanding will increase.

Speciation can be studied in the laboratory and in long-term studies in the field, but there is always a time limit. Now, with improved collecting and dat-ing techniques, paleontological studies of species evolution and species split-ting can be tied seamlessly to the present day, and we are beginning to see for the first time macroevolution in action.

New finds capture the headlines, but new insights into biomechanics, large-scale events, and macroevolution are even more impressive. The study of the history of life has never been more exciting than it is now.

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