The Fossil Record: Biological or Geological Signal?

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New species have appeared very slowly, one after another, both on the land and in the waters. Lyell has shown that it is hardly possible to resist the evidence on this head in the case of the several tertiary stages; and every year tends to fill up the blanks between them, and to make the percentage system of lost and new forms more gradual.   —Charles Darwin, *On the Origin of Species* (1859).

Darwin is referring here to Charles Lyell's famous nomenclature for the Tertiary System, in which the proportion of extinct to modern forms increased as one went back in time. He notes how new finds are plugging the gaps in the record. Charles Darwin famously devoted two chapters in *On the Origin of Species* (Darwin 1859) to the fossil record, and one of these was entitled "On the Imperfection of the Geological Record." Here he outlined the sequence of fossils in the rocks that showed how life changed from simple to more complex organisms up through the stratigraphic succession. He also highlighted the gaps in the fossil record, and reasons why every organism, and every species, would not necessarily be preserved. His main aim in covering these topics was to explain why the fossil record did not demonstrate a complete picture of the evolution of life, preserving all the intermediate forms demanded by his theory. And yet, Darwin ended with the hope that fossils would paint the pattern of the history of life as paleontologists continued their collecting efforts.

The next hundred years saw a to-and-fro in confidence about whether fossils could actually tell us much about the history of life. In reviewing this theme, Stephen Gould (1983) traced how Darwin's high expectations for the

fossil record were quickly dashed: paleontologists failed to identify many successions of fossils that told the story of evolution. Indeed, by 1909, most evolutionists saw the future in the new science of genetics, and could see little use for fossils. After the modern synthesis of the 1930s and 1940s, George Gaylord Simpson and others had shown that paleontology at least confirmed all aspects of Darwinian evolution, but perhaps could show nothing more. Gould characterizes the change through these years as a move from "irrelevance" in 1909 to "submission" in 1959. By 1982, Gould argued, in typical gung-ho style, that paleontology was truly in "partnership" with biology in delivering major insights on larger-scale patterns and processes that could never be predicted from a study of living organisms alone. At the time when Gould (1983) wrote, the "consensus paper" by Sepkoski and colleagues (1981) had just been published (see chapter 18 of this volume), and leading paleontologists seemed to agree that they could expect to find the large patterns of evolution from numerical studies of fossil databases. But where are we now?

Since 1981, there was perhaps a decade of relatively unchallenged development of statistical and empirical approaches to macroevolution and the fossil record, but concerns have since been expressed from two main directions. First, the growth of molecular phylogenetics cast doubt on patterns of relationships and dates from the fossils. Second, paleontologists themselves began to highlight the disturbing fact that the shape of the fossil record seems to map directly onto geological signals, such as the sea level curve or the volume of rock deposited. Could it be that paleontologists had been living in a fools' paradise, doggedly plotting patterns of fossils through time that told us nothing about evolution, but a great deal about sampling?

Note that, in this chapter, I concentrate on the larger-scale patterns that may be gleaned from the fossil record—global diversification and mass extinction, for example—and not the medium-scale, lineage-specific aspects of evolution, where quality and sampling concerns are rather different.

MOLECULES AND FOSSILS

The Molecular Clock

Fossils held the hegemony of deep time in evolution until 1962. In that year, in a classic paper, Emil Zuckerkandl and Linus Pauling made a modest proposal—that perhaps proteins and other molecules changed at predictable rates through long timescales. They later called this concept the *molecular clock*. It was known then, for example, that all vertebrates, and various other

organisms, possess the protein hemoglobin, which transports oxygen and makes our blood red. Human beta-hemoglobin is chemically identical to the hemoglobin of a chimp, but it differs in twenty-five of the 146 amino acid positions from the hemoglobin of a cow, in forty-five positions from the chicken, and in ninety-six positions from the shark. So, surely what this showed was that the amount of molecular difference was proportional to the time since any pair of species diverged from their last common ancestor. Humans and chimps diverged only a few million years ago, and so their hemoglobin has had little time to accumulate any changes, whereas humans and sharks last shared a common ancestor perhaps 500 million years ago, and so there has been 1,000 million years of independent evolution between the two.

The molecular clock was soon put to use as a tool in drawing phylogenetic trees, even though the labor in acquiring protein sequences in the 1960s was Herculean; the first such tree, with a set of proposed dates, was published by Vincent Sarich and Allan Wilson in 1967. These authors compared the hemoglobins of the great apes, showed that chimps were more closely related to humans than to gorillas or orangs, and as if that were not enough, suggested that the human and chimp lineages (evolutionary lines) separated a mere five million years ago. This predictably caused outrage on two fronts, but the date is our main concern. In 1967, paleoanthropologists were pretty clear that *Proconsul* from the early and mid-Miocene was on the human line, and that meant the split must have been fifteen to twenty million years ago. In the end, of course, the paleontologists reexamined their fossils and discovered that *Proconsul* was neither an ape nor a human, but an outgroup (relative of the ancestor) of both, and so it said nothing at all about the date of the chimp-human split. Even after four decades, the Sarich and Wilson (1967) date for the chimp-human split is pretty much correct, if perhaps slightly too young: the oldest human fossils are now *Sahelanthropus* and *Orrorin*, reasonably securely dated as six to seeven million years old.

Since 1970, and with a few such high-profile debates, most molecular studies have tended to confirm patterns of relationship established using fossils and morphological characters, and the order of branching in these trees has tended to match the order of fossils in the rocks. An uneasy truce existed, where molecular phylogeneticists and paleontologists might snipe at each other from time to time, but they agreed about most things. This perhaps uneasy coexistence came to an end rather dramatically in the mid-1990s, partly as a result of the increasing ease in obtaining molecular sequences, as well as an important renewal of interest in the computing algorithms used to draw trees, but also perhaps reflecting some mutual misunderstandings between both camps.

Molecular Age Doubling

A couple of papers published in 1996 perhaps exemplify the renewal of debate, and a sudden renewal of qualms about the quality of the fossil record. Gregory Wray, Jeffrey Levinton, and Leo Shapiro argued in a paper that attracted a great deal of interest that modern animal groups, ranging from sponges and corals at one end to vertebrates and echinoderms at the other, had originated some 1,200 million years ago, rather than 500–600, as the fossils indicated. This new date threatened the whole story of the rise of multicellular life through the late Precambrian, and especially the so-called Cambrian Explosion, the time when marine animals with skeletons suddenly appear in the fossil record at the beginning of the Cambrian Period, 542 million years ago. The headline message of the new paper was clear: animals had diversified 600 million years before the paleontologists thought, and so half the history of all those groups was simply missing. The new evidence understandably caused paleontologists to doubt their evidence: could it be that a crucial half of the record was missing?

The second paper was by Blair Hedges and colleagues, also published in 1996, and it looked at the timing of the origin of modern orders of birds and mammals. Here again the fossil record told a story of sudden diversification, this time after the demise of the dinosaurs some 65 million years ago. Birds and mammals have a rich fossil record in the Mesozoic, and both groups had long been known to have existed side by side with the dinosaurs. But these were primitive orders—toothed birds like *Archaeopteryx*, and an array of mammals of modest dimensions that were classified outside the modern orders. Hedges and colleagues presented their molecular evidence that modern birds and mammal orders had originated perhaps 120–130 million years ago, well before the first fossils. What was going on here? Paleontologists noted that the new molecular dates were roughly twice the fossil dates in both cases. Similar challenges followed through the 1990s, and to many commentators, the paleontologists were giving way. No longer could they claim that the fossil record told us the history of life—it told us only bits and pieces, and we didn't know which bits, so perhaps it was time for the hoary old fossil hound to hang up his hammer and leave the field to the molecular sequencers and their sparkling new labs.

Paleontologists responded in three ways at the time: either as ostriches, lapdogs, or mules. I hasten to classify myself as a mule in this. The ostriches, perhaps the majority of paleontologists, ignored the molecular challenge and rather hoped it would go away. The lapdogs accepted the new dates without

question and tried to find ways to accommodate their data: perhaps the molecular dates were the true dates and they recorded the moment of genealogical separation between major groups, but there had been a long cryptic history when the organisms were soft-bodied, rare, or living in restricted areas, and they then burst onto the scene much later, which marks their appearance in the fossil record. This is no explanation, of course, just a statement of ignorance, since it's unlikely a major group of organisms could sustain itself in obscurity for tens or hundreds of millions of years. The mules clung doggedly, or perhaps mulishly, to the view that the new molecular dates must be wrong, or at least that there must be a single story and both data sets—the fossils and the molecules—have to agree somehow. Were the ostriches, lapdogs, or mules right?

The Counter-Debate

Wray, Levinson, and Shapiro had drawn a new tree of relationships of the major animal groups based on particular genes they all shared, and they had calibrated the tree against spot dates from the fossil record. It was the calibration method that mattered. I remember reading their paper in 1996, and hearing the concerns of paleontological colleagues. I was inclined to doubt the new evidence, and oddly enough it was the easiest part of the exercise that gave rise to doubts. Sequencing genes and running the sequences through alignment and tree-building algorithms is a complex process, and methods are constantly debated and revised. Fixing the dates of the branching points has hitherto been a rather simpler procedure. Imagine a triangular elastic branching structure—fix it at the forked end, to represent the present-day groups, and then you can stretch it back as far as you like in time, using generally a single fixed point to date one of the nodes. Fix this calibration point at ten million years, and the tree stretches back to accommodate that. Fix the same point at fifty million years, and the whole tree stretches back five times as far.

Many people were concerned about the choice of calibration dates and, some years later, Kevin Peterson and colleagues showed a good reason for caution. Wray had used fixed dates from vertebrates to date the root of the animal tree. But vertebrate molecules evolve more slowly than those of nearly all other animal groups. So, this meant that Wray was using a slow molecular rate to project his estimates back in time, and the calculated date was much more ancient than it should have been. On recalculating, Peterson and colleagues (2004) found that the molecular evidence suggests a basal divergence of animal groups at 650 to 700 million years ago, much closer to the fossil es-

timates. There is still a time gap of 100 million years or so, and indeed this might be reduced on further recalculation of the molecular estimates or fossils may eventually be found that fill some of the gap.

What of the bird and mammal dates? Were they really twice as old as the oldest fossils, and was that first half of the fossil record of modern birds and mammals missing? Michael Foote and colleagues (1999) showed that the probability that fossils of modern mammalian groups would be entirely missing from huge spans of the Cretaceous was most unlikely, based on their preservation probabilities, and that is a reasonable statement of paleontological concern. Their view was countered by critics who argued that preservation probabilities for modern mammals in the Cretaceous were perhaps lower than those after sixty-five million years ago because either there were far fewer species and they were rare, or that the rocks were wrong (all marine), or that they were living in unsampled parts of the globe. But, in support of Foote, is the "missing mastodon" argument that I expressed in the same year (Benton 1999): we can go on explaining an apparent gap for so long, but eventually we have to accept that the missing taxon just isn't there, after searching hard and long. In the 1700s, some scientists explained the fossil bones of mastodon from Ohio as relics of living elephants that were yet to be found in some remote region in the American West. Eventually, of course, when all such remote areas had been explored, and no living mastodons were spotted, the bones had to be accepted as evidence of extinction. Paleontologists have identified a number (admittedly not many) of Late Cretaceous mammal localities, some yielding superbly preserved complete skeletons of placental and other mammals, but so far not a whisker of a member of a modern order.

Is there any sign of rapprochement between molecular and paleontological estimates for the branching of modern birds and mammals? There is still a substantial difference in the molecular and fossil dates for divergence of modern bird orders, although some unequivocal ducklike birds are now known from the latest Cretaceous, whereas before most such records were doubtful. The time gap is, however, still some twenty to thirty million years. A year or two ago it seemed that the mismatch in molecular and fossil ages for the modern placental mammals had been resolved, but perhaps not.

At one level the mammal paleontologists have not changed their position: there are indeed few, if any, fossils of mammals in the Cretaceous that can be assigned with confidence to a modern order. So, reputed records of basal monkeys, hedgehogs, and rodents living side by side with *Tyrannosaurus rex* and other dinosaurs are as dubious now as they always were. However, there are many Cretaceous records of placental mammals that lie outside the mod-

ern orders. Such fossils have been known for a long time, and they have been much enhanced recently by reports of complete specimens such as *Eomaia* from the 125-million-year-old Liaoning deposits of China. But these early forms cannot enlighten us about the molecules-versus-fossils debate because the fossils lie outside the tree of living groups. But there were some Cretaceous fossils that apparently lie within the tree of modern placental mammals but that do not belong to any modern mammalian order. These are the zhelestids, and possibly also the zalambdalestids, from Uzbekistan, described by Archibald, Averianov, and Ekdale (2001). The zhelestids were identified as basal relatives of the hoofed mammals and carnivores, while the zalambdalestids were said to be relatives of primates or rodents. These Uzbek fossils are dated as ninety-five to one hundred million years old, well down in the Cretaceous.

The eighteen or so modern orders of mammals are divided into four superorders: the Xenarthra from South America, the Afrotheria from Africa (of course), and the Laurasiatheria and Euarchontoglires from the northern hemisphere. Clearly, these four great superorders branched first in the early history of the placental mammals, perhaps from ninety to one hundred million yeas ago, and then, after the extinction of the dinosaurs, the modern orders flourished from sixty-five million years onward. So, the paleontologists had failed to sort out the deep relationships of the modern orders of placental mammals, and they had apparently failed to assign the Uzbek fossils, and some others, to their correct positions in the tree. Equally, the molecular biologists had perhaps been too quick to accept the first dates they calculated, and some had not fully grasped the difference between orders and superorders.

Sadly, this apparent consensus, or rapprochement, has been shattered by a full-scale cladistic analysis of the zalambdalestids and zhelestids by John Wible and colleagues (2007). They argue unequivocally that both groups of fossils from Uzbekistan lie low in the tree, outside the four great superorders of modern placental mammals, and that they tell us nothing about the timing of radiation of the modern groups. Further, they argue that none of the placental mammal fossils from the Cretaceous belong to modern orders or superorders, so the twenty- to forty-million-year gap between the molecular dates and the first fossils remains unbridged.

Partnership

Paleontologists and molecular biologists share two major enterprises: drawing the tree of life and dating it. There is only a single tree, and each branching point must have a single date, in my view. Are we doomed to continuing

spats like those just described? Practitioners in both fields need to respect each other and exercise caution. First results are not always correct results, especially if they contradict everything that has been put together by generations of other scientists. The morphologists and paleontologists tussled with the tree of placental mammals for years, and they failed miserably to resolve deep relationships. Then, molecular phylogeneticists discovered the Afrotheria in 1997, and the remainder of the tree fell into place rapidly. Numerous independent molecular investigations confirm the tree, and paleontologists are still puzzling over the morphological evidence for the new superorders. What is it that elephants, dugongs, hyraxes, tenrecs and golden moles share— apart from having originated in Africa? The schnozzle? Maybe. They all seem to share the character of testicondy, retention of their testes in the abdomen, and not exposed in a scrotal sac—but this might be the ancestral character of all mammals. Maybe no one will ever identify the morphological character that unites Afrotheria—perhaps they just evolved so fast in the Cretaceous that they never acquired a unique character, or such a character or characters has been lost, overwritten by their very different patterns of evolution since. Even the most hard-bitten paleontologist has to admit his or her data are not up to the task here.

In dating the tree, it seems to me there is a clear partnership. The to-and-fro debate about dates is daft. The irony, on the one hand, has been that molecular phylogeneticists have promoted their own calculated dates against the perceived weakness of existing paleontological dates—or should that be *most* existing paleontological dates, because at least one paleontological calibration date is needed to date the tree, and such calibration dates have sometimes been treated as some kind of holy grail, immune to challenge or criticism.

The partnership in dating the tree of life is simple: paleontologists supply as many dates as they can, and these are vetted for consistency and then used in multiples to determine otherwise unknown dates. Multiple dates and vetting are important. Paleontologists have a sense of which dates they can determine with some confidence, and which might be rather weak. But it's possible also to take a set of best-estimate dates and assess them for consistency, or congruence, on an established tree: if any should appear to be wildly out of line with the others, by being either too young or too old, they can be rejected. Then, the set of congruent dates can be used to determine missing dates. The weakness of this approach is, of course, that all the paleontological dates might be congruent because they are all too old or too young by the same amount. Equally though, such errors might emerge on subsequent checking with other sets of dates.

What of the dates produced by paleontologists? Up to now, most, but certainly not all, molecular phylogeneticists have tended to use point dates, without error bars. Many now try to encompass an error term in their calculations, say plus-or-minus five% of the age. I have been studying this issue with Phil Donoghue, also at the University of Bristol, and we have realized that the distribution of uncertainty around a fossil date is not symmetrical, a point made previously by Robert Reisz, Johannes Müller, Marcel van Tuinen, Elizabeth Hadly, and others (Reisz and Müller 2004; van Tuinen and Hadly 2004). In fact, it is possible to give a rather accurate minimum constraint on the date based on the oldest known fossil in a clade (that is, the oldest definite fossil, ignoring scrappy and uncertain remains that might be older). Then, the distribution of probability on the date follows a logistic, or S-shaped, curve (fig. 2.1), mapping the rough shape of diversification of the group back to a point where there are no more fossils, even dubious ones, and one or more fossil beds can be identified that ought to contain fossils of the clade in question, but do not. Molecular phylogeneticists have methods to accommodate distributions of dates like this, with a so-called hard minimum constraint and a soft maximum constraint. We hope these developments (Benton and Donoghue 2007) mark a new era of collaboration across the systematics community, where molecular biologists and paleontologists each do what they are best at, and by combined efforts perhaps come closer to a reasonable estimate of the truth than has been possible up to now.

PLOTTING THE FOSSIL RECORD

A Biological Signal?

As noted at the start of this chapter, Charles Darwin assumed that the fossil record, plagued with gaps as it was, would show the shape of the history of life. And that is broadly the popular perception, too. Reports of new fossils and studies of mass extinctions in the press generally accept the dating of those fossils or events, and any statements about the shape of an evolutionary pattern inferred from the new discovery.

This common perception is based on qualitative evidence, and that qualitative evidence satisfies most paleontologists, and indeed most nonpaleontologists in the scientific community. The key observation is that new fossil finds rarely rewrite the textbooks, although we all conspire with our institutional publicity offices when they feed that line to the press. In fact, Darwin knew about early Paleozoic trilobites and brachiopods, Silurian and Devonian fishes,
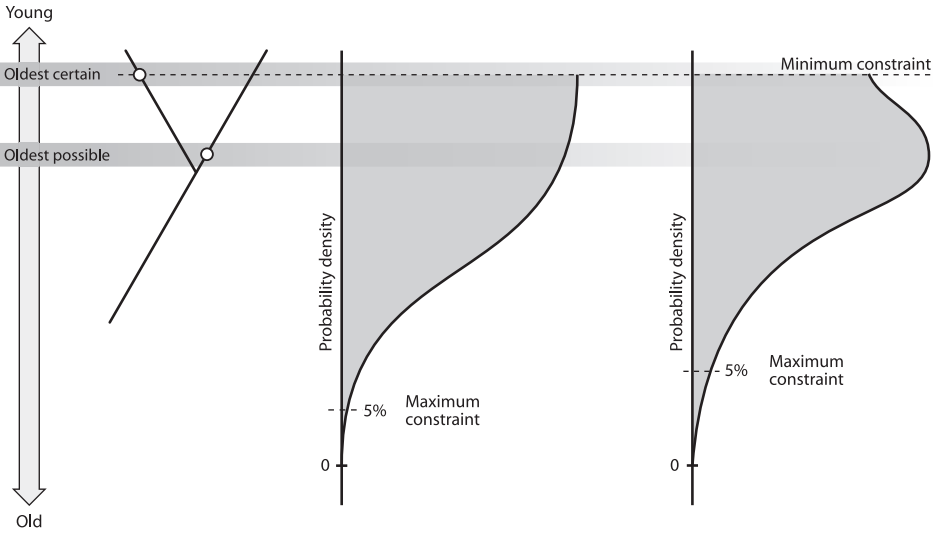
Figure 2.1 Discordances between morphological disparity and taxonomic diversity under different evolutionary scenarios. Top row, idealized diversity patterns. Bottom, predicted diversity and disparity curves over time (solid line, taxonomic diversity; dashed line, morphological disparity). (A) Morphological evolution is constrained though not fully inhibited; taxonomic diversification is not accompanied by morphological diversification. (B) Morphological steps are large early in the clade's history; morphological diversification outstrips taxonomic diversification. (C) No constraint on morphological evolution, no trend in morphological step size; morphologic diversification is concordant with taxonomic diversification. From Wesley-Hunt (2005).

Carboniferous trees, giant insects and tetrapods, dinosaurs, Mesozoic mammals, *Archaeopteryx* (the oldest bird, then and now), Eocene horses, and so on. The two big areas of wholly new discoveries since 1860 are Precambrian life and human fossils. But, were the fossil record a patchy *and misleading* record, one might expect some real surprises, like a Carboniferous dinosaur or a Triassic trilobite. So, I would argue, the record may be patchy, but it is not necessarily misleading.

This was borne out by quantitative studies through the 1990s. A number of paleontologists realized that they had the remarkable good fortune to have at their disposal two, or arguably more than two, independent sources of data on the history of life. Not only are there the fossils in the rocks, there are also phylogenetic trees. A phylogenetic tree may contain fossil species, or it may be based entirely on living forms. The tree is drawn up by quantitative analysis

of character data, either morphological or molecular. So, the age of a fossil has no influence on the placement of a species in the tree—its placement is based entirely on rationalizing the character distributions until they fit a single tree solution best. The disjunction between fossils in the rocks and phylogenetic trees is especially clear in the case of molecular trees that are produced entirely from protein or nucleic acid sequences of living organisms. It would be a wonder if molecular trees gave the same sequence of events as the order of fossils in the rocks—and yet they normally do!

This was first shown by Mark Norell and Mike Novacek from the American Museum of Natural History in 1992, who found that 75% of trees of mammals agreed significantly with the order of fossils in the rocks. Now, this is not meant to be a test of the fossil record, assuming the trees are correct, nor is it a test of the quality of the trees, assuming the fossil record is correct. It's an assessment of congruence between two data sets. If they disagree, then there is no way to tell whether the tree or the fossils, or both, are wrong. But if the trees and the fossils agree, then it's hardly credible to claim that one or other is at fault. Congruence in such a case indicates that both methods, based on different kinds of data, are telling the same, true, story.

After this analysis, several groups began pursuing this approach, and in the end, my colleagues Matt Wills and Becky Hitchin and I accumulated a set of 1,000 trees and fossil records spanning all groups of organisms, plants, animals and microbes, through the last 600 million years of geological time. We looked at congruence between trees and fossils using many different approaches and found remarkable levels of agreement, and the agreement seemed comparable for different groups of organisms and through geological time (fig. 2.2). In a 2000 paper, we argued that this confirmed that the fossil record gave us the correct broad pattern of the history of life, and that the quality of the record did not diminish markedly back in time.

This last finding was a surprise to us and everyone else. It is a commonplace observation that fossils are abundant and easy to collect in the Cenozoic, but obscure and rare in the Cambrian. Fossils are rarer in older rocks because large volumes of those older rocks have been lost to burial beneath younger rocks, subduction, folding, pressure, or erosion, and these processes often damage or destroy any fossils that can still be collected. So how can the trees versus fossil ages congruence measures be the same for truly ancient and less ancient fossil records? The answer has to do with the scale of observation. At the local scale, working in a quarry and collecting individual specimens, there is no doubt the fossil record gets worse with increasing age. However, at the global scale, and the levels of stratigraphic stages (mean duration seven
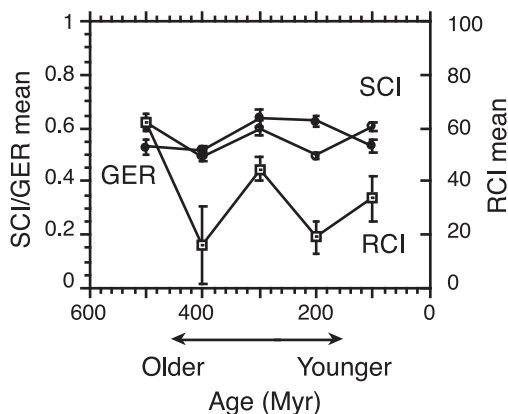
Figure 2.2 All possible combinations of evolutionary tempo and mode have been recorded from the fossil record. Research is sorely needed on whether clades vary in their frequencies of the different combinations, and if so, why. The upper left quadrant is classic phyletic gradualism, the lower right is punctuated equilibrium.

million years) and genera or families (not species or specimens), the quality of the fossil record seems constant—maybe constantly good or constantly bad, but constant nonetheless.

Critics have pointed out that all we were measuring was the proportion of the fossil record that is known. The contrast to be grasped is between the diversity of life as it actually was in the past, and the sample represented by fossils (namely, the fossil record). So, it could be that the fossil record documents 80% of the life of the Miocene, but only 5% of the life of the Cambrian—and this is quite likely. Our clade-versus-age measures might show that we have uniform coverage of the fossil record through time, but that would not address the issue of the overall very weak documentation of the Cambrian. Our response is that clade-versus-age measures are applied to cladograms, and those cladograms can include fossilizable and unfossilizable organisms. So, a tree based on modern organisms can extend back in time as far as the Cambrian, for example, and indicate that jellyfish or worms were there; their absence as fossils would then translate into a major gap that would lower the values of the clade-versus-age metrics. Nonetheless, the use of clade-versus-age metrics does not provide a strong link between reality and the fossil record, because it presumably works less and less well the further back in time one goes.

If this is the case, it confirms the assumptions made in the consensus paper by Sepkoski and colleagues (1981) that the fossil record retains enough of a

biological signal that we can use it to study some aspects of evolution. But that consensus has been challenged by some paleontologists in the past ten years.

A Geological Signal?

First, John Alroy and colleagues (2001) have suggested that sampling might diminish markedly back in time. Here they are resurrecting the view expressed by David Raup in his classic 1972 paper where he outlined all the reasons, some of them just indicated, why the decline in marine diversity back into the Paleozoic is not a real signal, but actually documents the ever-worsening quality of sampling. John Alroy and colleagues have presented numerous statistical studies based on sectors of the fossil record that appear to support this view. If they are correct, the fossil record presents more a geological signal than a biological signal. Is there independent evidence for such a claim?

Shanan Peters and Mike Foote argued in 2002 that the fossil record largely mimics the distribution of rocks. They plotted extinction and origination curves against the number of named stratigraphic formations in the United States. At times when diversity and origination were apparently high, so too were the numbers of formations; at times of extinction, the number of named formations plummeted. They interpreted this to mean that our record of the diversity of fossils through time is based largely on the volume of available rock, or at least the volume of studied rock. The more paleontologists work on rocks of a particular age, the more fossils they find and the more formations they name. If fossil volume mirrors rock volume, what might control that?

Sea level might be the driver. Through time, global sea levels have risen and fallen, and at present we are in a time of relatively low sea levels because huge volumes of water are locked up in polar ice. In the Cretaceous, for example, when there was no, or very little, polar ice, sea levels were up to 200 meters higher than today. When sea levels are high, more marine rocks are deposited, especially on the continental shelf, where life is most abundant. So, when sea level rises, the volume of marine rocks deposited worldwide increases, and so too does the apparent diversity of life in the sea. The corollary might be that when sea levels are high and marine fossils are being buried in abundance, there should be low levels of deposition and fossil preservation on land, a view suggested by Peters and Foote (2001; [Equally, high sea levels might mean the continents become more fragmented, and so endemism increases, and global diversity on land could also increase]).

The sea level idea has been tested by Andrew Smith (2001, 2007) and Emmanuel Fara (2002). Smith found that the marine fossil record of much

of the Mesozoic largely mirrored the sea level curve, and there is no doubt that particular rises and falls in apparent diversity must relate to particular up and down movements of the sea. But Smith found that the global marine diversity curve diverged from the sea level curve over the past one hundred million years: as sea levels have steadily fallen through that time, marine diversity has rocketed. Further, Fara found no inverse correlation between the sea level curve and the apparent diversity of life on land. The prediction that rises in sea level might be matched by falls in terrestrial diversity, and vice versa, just did not happen.

So, if the rock and fossil records are linked to some extent, but not completely, is one driving the other, or are both driven by a third cause? Following publication of his paper in 2002, I commented to Mike Foote at a conference that the linked patterns might not indicate that rock volume was driving fossil diversity, but perhaps the opposite. It might well be that geologists name lots of formations when fossils are abundant, and name fewer when fossils are rare. That was perhaps a cheeky volte face of the rocks-drive-fossils argument, but Shanan Peters (2005) has now resurrected an older idea first suggested by Jack Sepkoski and others in the 1970s (Sepkoski 1976; Flessa and Sepkoski 1978), and even by Norman Newell (1967) with regard to extinctions, that the linked formations/fossil richness curves might be driven by a third common cause—maybe sea level change, or maybe sea level and continental plate movement. The point is then that the matching curves are giving *both* geological and biological signals, not merely a geological signal that masks any biological signal. The *common-cause* hypothesis of Sepkoski, Peters, and others is that times of high sea level and voluminous sediment deposition were also times of rich life in the seas, and so both rocks and fossils are abundant. There is an analogy here with the long-established species-area effect in ecology: large islands support many species, while small islands support few.

PERSPECTIVE

I have never doubted that the fossil record tells the story of the history of life, and neither did Jack Sepkoski. The 1981 consensus paper may have been naive in some ways—after all, the five matching patterns just proved that the five samples of the fossil record matched, not that this was the true pattern. All five databases, whether sampling fossil species, genera or families, or trace fossil diversity, were all sampling from the same rocks, although the sampling methods differed. So the sampling was congruent, but was the record in the rocks anything like the true biological pattern? What about those episodes in

Earth history when no rock has been preserved and so we have a complete blank? What about those groups of soft-bodied, or microscopic, organisms that we know nothing about? This is impossible to assess because what is required is a comparison of the known (i.e., the fossil record) with the unknown. There are perhaps two responses to this point that I believe to be correct, though neither is decisive.

The commonest response would be to say that modern oceans and landscapes contain a mixture of readily fossilizable, and essentially unfossilizable, organisms. We know the soft-bodied and microscopic groups today, and so these can be restored for past times. So, we know the Ordovician ocean was populated by brachiopods, trilobites, corals, sea lilies, and bryozoans, and it can also be assumed to have harbored jellyfish and worms. And indeed, sites of exceptional fossil preservation, such as the Burgess Shale or the Solnhofen Limestone, provide some kind of test: we know the jellyfish and worms from those times because they are occasionally preserved. We just have to join the dots a little more in reconstructing the evolution of such soft-bodied groups. The sites of exceptional fossil preservation suggest that the proportions of skeletonized to nonskeletonized organisms were pretty much the same in the past as they are today, so perhaps this conservative assumption can be applied to fill out the known fossil record.

The second answer comes from our work on comparing trees and fossil records. Trees contain a mix of readily fossilizable and unfossilizable organisms. Indeed, a molecular tree can be constructed for worms or jellyfish just as readily as for clams or fishes. A tree of entirely soft-bodied organisms clearly cannot be compared with the fossil record because there is little or no fossil record. But a tree of entirely skeletonized organisms can be compared with one that mixes skeletonized and nonskeletonized organisms, such as a tree of all animals. Both kinds of trees match the fossil records equally well. There is no evidence (yet) from molecular trees that massive sectors of biodiversity are being missed or that such soft-bodied organisms, if we knew them, would entirely turn our picture of ancient ecosystems on its head.

I see a golden future for paleontology in drawing and dating the tree of life, in seeking to understand major diversifications and extinctions, trends, large-scale ecosystem shifts, and the dance of faunas and floras as continents and oceans moved stately around the globe. The challenges to fossil record quality are good for the vigor of the subject, and sampling standardization is crucial. However, it would be wrong to overstate the problems: paleontologists can confidently follow Jack Sepkoski in celebrating and promoting their astonishing database on the history of life.

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