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Derek Turner
Excerpt
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1 Introduction

Paleontology and evolutionary theory

A world without fossils

Imagine a planet almost exactly like ours, but with one crucial difference: it has no fossils. Call this imaginary planet *Afossilia*. Afossilia and Earth harbor the very same kinds of living things, from ferns to human beings to *E. coli* bacteria. Both planets have the same surface features and the same types of rocks. And both have experienced exactly the same evolutionary histories, with the same species evolving and going extinct at exactly the same time. We can even suppose that you and I have counterparts living on Afossilia – that is, that there are people there who are exactly (or almost exactly) like us.

Some Biblical literalists hold that God placed fossils in the rocks in order to test our faith in scripture. I invite you to join me now in thinking about a simple inversion of this familiar idea: what if God – or if not God, then some more sinister spirit – systematically removed all the fossils from the rocks just before (Afossilian) humans evolved and began to study the world around them. Afossilia has no fossilized footprints, leaf imprints, shells, pollen, teeth, bones, coprolites (fossilized feces), or any of the remains of ancient organisms that we on Earth can see on display in natural history museums.

Suppose you had the opportunity to tour a major research university on Afossilia. There you would find physicists, cosmologists, astronomers, chemists, biochemists, and molecular biologists doing exactly the same things that scientists in those fields do here on Earth. But you would find no paleontologists on Afossilia – no departments of paleontology or professional associations for paleontologists. A world without fossils must also be a world without paleontology ("the study of ancient beings"). The natural history museums, if there were any at all, would contain exhibit halls full of rock and mineral samples, as well as stuffed and pickled specimens of creatures living today, and not much else. *Jurassic Park* never appeared in Afossilian theaters, and Afossilian children have no dinosaur toys or books.

At the end of the day, this thought experiment might not turn out to be fully coherent – a common problem with philosophical thought experiments. Thought experiments often ask us to imagine scenarios that seem logically possible, but which gradually stop making sense if you ask the right awkward questions. You may already be thinking of problems with this one. For example, do the Afossilians have any fossil fuels? What exactly does "fossil" mean in the first place? (I return to that issue at the end of the book, in Chapter 10.) For now, we need not worry too much about the details. An imperfect thought experiment can still serve as a useful device for generating philosophical questions.

What would Afossilian biology look like? And in particular, what would the Afossilians think (or be justified in thinking) about evolution? Would their views about evolution differ from the views of scientists on Earth? Important parts of Afossilian biology would be just like biology here on Earth. For example, the Afossilians would probably have much the same understanding of genetics and microevolutionary change that we do. Nothing would keep them from studying the ways in which natural selection, drift, mutation, and migration can lead to changes in gene frequencies in populations. But what could the Afossilians know about large-scale evolutionary change? Can scientists learn anything about evolution from the fossil record that they simply cannot learn in any other way?

Organismic *vs.* evolutionary paleontology

Paleontologists use fossils to try to understand the history of life on Earth. The term "paleontology" literally means the study of ancient being, and it is sometimes contrasted with "neontology," which refers to the study of life as it exists on Earth today. We can draw a rough distinction between two kinds of research that paleontologists do. The first kind of work, which I will call *organismic paleontology*, attempts to answer questions about the behavior, the biology, and/or the ecological role of some specific type of prehistoric creature. *Evolutionary paleontology*, by contrast, focuses less on questions about specific kinds of prehistoric life, and more on questions about the nature of large-scale evolutionary patterns and processes. This book will deal mainly with evolutionary paleontology.

Figure 1.1 *Tylosaurus dyspelor*. This restoration of a mosasaur appeared in an early paper by Henry Fairfield Osborn (1899), of the American Museum of Natural History.

In order to make the distinction between organismic and evolutionary paleontology clear, it will help to consider examples of each of these two kinds of paleontological research. From there, I will go on to develop some of the questions that will take up the rest of the book.

First, an example of organismic paleontology: the term “mosasaur” means “reptile of the Meuse,” and the first mosasaur remains were found in a quarry near the Meuse River in Holland in the late 1700s. The mosasaurs were not dinosaurs, although they flourished during the Cretaceous period, the heyday of the dinosaurs. Instead, the mosasaurs were intimidating marine reptiles – the archetypal prehistoric sea monsters (see Figure 1.1). The very largest ones grew to lengths of 45–50 feet, though most were smaller. The mosasaurs became extinct at the same time as did the non-avian dinosaurs, around 65 million years ago. Their remains have been found in Mesozoic rocks all over the world (Bell 1997). Did the mosasaurs spend most of their time in the deep oceans? Or did they live near the surface? How fast and how far did they swim? Since we cannot travel back in time to observe the animals in action, scientists have to use ingenious techniques to bring them back to life.

Consider the question of how fast mosasaurs could swim. Could they engage in sustained, fast swimming over long distances in the open ocean? Massare (1988) showed that mosasaurs probably could not swim very efficiently. She began by calculating the *fineness ratios* of different kinds of Mesozoic marine reptiles. The fineness ratio (F) is defined as the ratio of body length (L) to mean diameter (W).

$$F = L/W$$

Every marine animal has a fineness ratio, and one can easily estimate the fineness ratios of living creatures. For example, bottlenose dolphins have a fineness ratio of 4.4. Swordfish have a fineness ratio of 4.2. One can also estimate the fineness ratios of extinct creatures simply by measuring their skeletons.

The fineness ratio is related to the amount of drag that an animal must overcome during swimming. There are different kinds of drag, but the main one to think about is friction drag, which results from the flow of the water over the animal's body. If you could hold the body volume constant while increasing the fineness ratio, that would also increase the surface area – and the more surface area, the more drag. Scientists studying living organisms have shown that friction drag is minimized when the fineness ratio is about 4:5. The optimal range for fineness ratios is between 3 and 7. An animal with a fineness ratio lower than 3 or higher than 7 swims less efficiently, because drag increases considerably. If you have two animals, both swimming at the same speed and for the same length of time, the one that experiences greater friction drag will have to expend proportionally more energy to keep up. It's no coincidence that dolphins and swordfish have fineness ratios well within the optimum range, since both species engage in sustained fast swimming. Many other modern day swimmers, such as crocodiles and eels, have fineness ratios that are well outside the optimum range.

What about the mosasaurs? They also had fineness ratios well outside the optimum range – some in the neighborhood of 10 or 11. Massare's conclusion: mosasaurs would have been fairly lousy long-distance speed swimmers. This biomechanical finding might have some implications concerning what they ate and how they lived. Massare argues that they were probably ambush predators, and that their body type would have been better adapted for burst swimming and quick, lunging attacks.

Now contrast Massare's work on mosasaurs with an example of evolutionary paleontology. Many of the questions that evolutionary paleontologists work on have to do with extinction. Extinctions do not seem to be completely random; some species have a higher probability of becoming extinct than others. So what sorts of things might influence a given species' probability of becoming extinct? Incidentally, this is a question that interests conservation biologists as well as paleontologists, but the fossil record gives paleontologists a unique way of investigating it. One thing that might play a role here is the relative abundance of different species. Intuitively, it would seem like numbers can make a difference to extinction risk: a species that is rare would seem to be at greater risk of extinction, whereas a more abundant species seems more insulated against extinction. Indeed, at first glance, it seems like the relationship between abundance and species risk ought to be linear: the more a species increases in number, the more its extinction risk is reduced. After all, extinction is what happens when the population size falls to zero. So the further away from zero a given species is, the lower its risk of extinction.

In one recent study, Simpson and Harnik (2009) set out to test this idea that the relationship between species abundance and extinction risk is linear. Notice, though, that this is not the kind of claim that one can test by going out into the field and hunting for a particular fossil. Instead, Simpson and Harnik used an approach that was pioneered in the late 1970s and early 1980s by Jack Sepkoski, a paleontologist who was based at the University of Chicago (Ruse 1999). Sepkoski was the first scientist to use large computer databases as a tool for paleontological research. He found that if you have a database with detailed information about thousands of fossil specimens – all of which had been collected and painstakingly described by earlier scientists – then you can use the database to search for interesting patterns in the fossil record, a technique that Michael Ruse has aptly termed "crunching the fossils." Simpson and Harnik took advantage of the Paleobiology Database (PBDB), a publicly accessible and constantly growing reservoir of information about fossil collections from around the world. Simpson and Harnik focused on marine bivalves over the last 250 million years. Although many people immediately think of dinosaurs when they think of paleontology, evolutionary paleontologists tend to focus more on marine invertebrates, just because they leave behind lots and lots of fossils. To give an idea of the scope of Simpson and Harnik's study, they trolled through 1,631 different collections of fossils around the world, and together those collections housed 7,169,465 fossils.

What Simpson and Harnik found was highly counterintuitive. Instead of a linear relationship between species abundance and extinction risk, they found the U-shaped curve depicted in Figure 1.2. Extinction risk does increase with rarity. But at the same time, species that are *too abundant* also seem to have an increased risk of extinction. Much of Simpson and Harnik's work is devoted to analyzing possible sources of error and bias, just to make sure that their result is not a statistical illusion. The big question at the end, of course, is why superabundance comes with increased extinction risk. What is the cause of this "anomalous yet persistent" pattern that seems to be showing up in the fossil record of marine bivalves? They decline to speculate, preferring instead to leave the "why" question for future research.

In both of these case studies, the scientists employ rigorous quantitative techniques. Massare uses biomechanical modeling to help answer questions

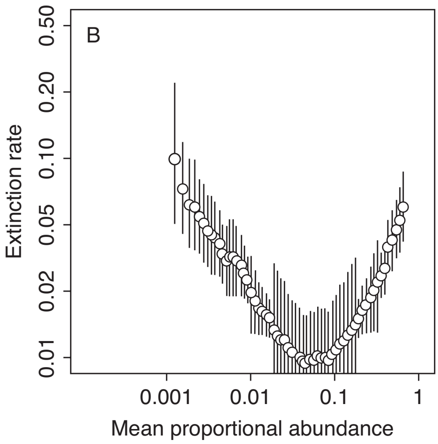

Figure 1.2 Simpson and Harnik's (2009) U-shaped curve. The proportional abundance of a genus is the ratio of its abundance to the total sample size of a fossil collection. The mean proportional abundance for a genus is arrived at by taking the average across many collections. For discussion of the details of calculating the extinction rate, see Simpson and Harnik (2009, p. 633). As the mean proportional abundance increases, the extinction rate drops, and then increases again. Reprinted with permission of the Paleontological Society.

about mosasaur swimming behavior, whereas Simpson and Harnik use sophisticated statistical tests to check the hypothesis that the relationship between abundance and extinction risk is linear. Yet Massare is investigating questions about mosasaurs, while Simpson and Harnik are investigating questions about evolution. These different emphases help explain why the scientists work with such different data sets. Massare needs only a few mosasaur skeletons to supply measurements of fineness ratios, but Simpson and Harnik need to look at millions of fossils in order to discern larger evolutionary patterns.

The paleobiological revolution

In the early 1970s, a number of paleontologists had grown dissatisfied with the position of their discipline on the sidelines of evolutionary theory. They set out to change things. The best-known member of that group was Stephen Jay Gould, but it included a number of other leading scientists as well: J. John Sepkoski, Jr., David Raup, Thomas J.W. Schopf, Steven Stanley, Elisabeth Vrba, Niles Eldredge, and others. These ambitious scientists helped to bring about what historian of science David Sepkoski has called "the paleobiological revolution" (Sepkoski 2009a). Not that there was nothing interesting going on in paleontology before the 1970s. Many of the scientists just mentioned took inspiration from the work of George Gaylord Simpson, a paleontologist of the previous generation whose classic text, *Tempo and Mode in Evolution* (1944), helped to clarify basic questions and concepts that would shape much of the research that paleontologists would go on to do. Simpson sought to show how paleontology fitted into what is known as the "modern synthesis" of Darwin's evolutionary theory with classical genetics – that is, how it fitted in with the latest and best thinking about evolution at the time.

Though influenced by the work of Simpson and other mid-century scientists, the "revolutionaries" of the 1970s went further. This new generation of scientists aimed to shake things up in at least seven different ways. Evolutionary paleontology as we know it today is largely a result of their efforts. I'll try to capture the spirit of the young Turks of the 1970s and 1980s with seven revolutionary slogans.

"*Paleontology has more to contribute to biology than to geology*." Paleontology has always occupied an awkward position between these two sciences. The study of fossils has long played an important role in geology, in part because understanding fossils is helpful for identifying and dating types of rocks. The 1970s revolutionaries sought to move their field closer and closer to biology, and one way in which they tried to do that was to show that they had something to say about evolutionary theory. They founded a new scientific journal in 1975, called *Paleobiology*, in order to provide an outlet for studies of the fossil record that addressed questions about evolution. Some started using the term "paleobiology" to describe their work. This was a way of signaling that the game had changed; paleontologists were now contributing to evolutionary theory.

"*Study fossils in bulk – individual specimens don't tell you much about evolution*." A single fossil find can sometimes have the effect of dramatically changing our views about prehistoric life. One such find was John Horner's discovery of dinosaur nesting sites that forced a rethinking of dinosaur social life (Horner and Makela 1979). For all the excitement that attends those discoveries, it remains true that the best way to investigate general questions about how evolution works is to study huge collections of fossils in order to identify patterns. Jack Sepkoski's use of large databases represents an important innovation in this direction. Rather than seeking out the exciting individual fossil finds, these scientists turned to statistical techniques for describing and analyzing larger patterns in the fossil record.

"*Paleontology needs theories*." In the physical sciences, there has long been a distinction, though not a sharp one, between two sorts of activities. On the one hand, there is the activity of making novel theoretical contributions, of coming up with new ideas and new ways of seeing things. Then there is the more workaday activity of designing and overseeing experiments, taking measurements, collecting data, building new experimental apparatus, and so on. Although both of these activities are obviously important, the more theoretical work has long been accorded higher prestige. (If you name a few highly regarded "scientific geniuses" off the top of your head – Isaac Newton, Charles Darwin, Albert Einstein – one thing they all had in common was that they all did theoretical work.) Up until the 1970s, paleontology had no theory of its own. There was, of course, evolutionary theory, which is based on the work of Darwin and Gregor Mendel, but paleontology had not (yet) contributed much to the shaping of that theory. The new paleobiologists set out to show that their science had a theoretical contribution to make. The 1970s and 1980s saw the development of new theoretical approaches, especially punctuated equilibria (hereafter PE) and species selection. Paleontologists began to argue that the fossil record requires the revision and/or expansion of traditional evolutionary theory.

"*If you can't experiment, then simulate*." Paleontologists are hampered to some extent by their inability to perform direct experiments on the past (Turner 2007). However, in the early 1970s, a group of scientists met at the Marine Biological Laboratory in Woods Hole, Massachusetts, and developed the first computer simulation of large-scale evolutionary processes (Huss 2009). It became possible to test ideas about evolution by running virtual experiments. These new modeling techniques had a major impact on paleontology, especially with respect to scientists' thinking about the role of chance and randomness in evolution. The computer models made it possible to study chance in a way that no one had ever done before.

"*Don't just assume that the fossil record is incomplete; analyze the incompleteness*." When Darwin first published the *Origin of Species* in 1859, he had to explain away the fact that no one had found any intermediate forms in the fossil record – no "missing links" between older species and newer ones. So he argued that the geological record is incomplete, and that geological processes erase a great deal of information about prehistoric life. This move, as much as anything else, helped to nudge paleontology to the sidelines of evolutionary theory. If the fossil record is so incomplete, what does it have to teach us about evolution? In the 1970s and 1980s, paleontologists began to challenge this assumption of incompleteness in various ways. The theory of PE represented one kind of challenge (see Chapters 2 and 3). But scientists also insisted on making the incompleteness of the fossil record itself into an object of study. Once we understand some of the sampling biases in the fossil record, we can correct for them. Philosophers use the term "epistemology" to refer to the theory of knowledge. These scientists wanted to make the epistemology of paleontology a part of paleontology itself. Studying the incompleteness of the fossil record is a way of studying the limits of our knowledge of the past.

"*Resist reductionism*." In the mid twentieth century, once the modern synthesis in evolutionary biology was well established, many scientists took a reductionist view of the relationship between *macroevolution* and *microevolution*. Microevolution consists of changes in gene frequencies in populations – the sorts of changes that modern evolutionary theory describes and explains so well. Macroevolution is any change that occurs above the species level, such as increasing biodiversity (that is, increasing numbers of species). The mid-century reductionists tended to think that macroevolution is "nothing but" microevolution. If you could understand the causes of all the microevolutionary changes taking place over vast sweeps of evolutionary time, then you would know all there is to know about macroevolution. The new generation of paleontologists in the 1970s and 1980s launched a sustained attack on this reductionist outlook. They argued that there are some macroevolutionary patterns and trends that could not be mere by-products of changes taking place at the microevolutionary level. Some pushed for a newly expanded hierarchical view of evolution, which would allow for irreducible mechanisms operating at the macro-level. The centerpiece of this new hierarchical view was the concept of species selection (Chapters 4 and 5).

"*Don't shy away from raising big questions about evolution*." How important is natural selection as a cause of evolution? To what degree is the course of evolutionary history a matter of chance? Is evolution progressive? Was the evolution of intelligent, language-using, tool-using, creatures like us inevitable in the end, or do we owe our existence to historical accidents? Some of the new paleobiologists thought that the fossil record holds the key to answering some of these questions.

Hopefully this sketch captures some of the spirit of the new paleontology that emerged in the 1970s and 1980s. Not all of the scientists involved in these new developments would have endorsed all of these slogans, and they have not always agreed about what the new science should look like. David Sepkoski (2005; 2009a) has written about this little-known scientific revolution in much greater detail, from an historian's perspective. In many respects, the paleobiological revolution represented a move in the direction of evolutionary paleontology. In saying this, I don't mean to suggest that the scientists necessarily wanted to move away from organismic paleontology. The study of particular kinds of prehistoric life remains an important and lively part of paleontology. Questions about evolution often turn out to have connections with questions that call for organismic reconstruction. It would be a mistake to think of the paleobiological revolution as a revolution against organismic reconstruction. Rather, the major players of the "revolutionary" period – the 1970s and 1980s – sought to establish evolutionary paleontology as an important part of the field, without necessarily edging out other things.

Perhaps more than any other scientific field, paleontology today has a complicated relationship with its public image. For one thing, paleontology has a special role to play as a gateway science. Many young people first get excited about science through reading dinosaur books, visiting natural history museums, or watching dinosaur specials on television. Journalists are often quick to report on the latest dinosaur discoveries, and a number of dinosaur scientists, including Robert Bakker and John Horner, have written popular books about their work. My impression is that many paleontologists are quite happy that their field has such a high profile in the wider culture. This high profile does have a downside, however. For one thing, it's natural that when most people think of paleontology, they think of organismic reconstruction in general, and of dinosaur science in particular. (I should add that not all dinosaur science involves organismic reconstruction, but much of it does.) Evolutionary paleontology, with its more theoretical bent, remains less well known. In many ways, dinosaur science remains paleontology's public face, even though much of the action over the past forty years – not *all* of the action, but a lot of it – has occurred in evolutionary paleontology.

Paleontology's high public profile has another downside as well. Within the natural sciences, and possibly within academia more broadly, there is a widespread prejudice against those who write for broader, non-academic audiences. The general thinking behind this prejudice seems to be something like the following: "If non-specialists can understand it without too much effort, then it must not be that serious." Or maybe the thinking is like this: "Why