

From Old Objections to Novel Explanations: Darwin on the Fossil Record

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Abstract

The ninth and tenth chapters of the *Origin* mark a profound, if perhaps difficult to detect, shift in the book's argumentative structure. In the previous few chapters and in the ninth, Darwin has been exploring a variety of objections to natural selection, some more obvious ("where are all the fossils of transitional forms?") and some showing careful attention to challenging consequences of evolution ("could selection really produce instincts?"). Starting in the tenth, however, Darwin turns to showing us what kinds of new and unexpected results evolutionary theory might be able to offer us, again in domains both predictable (extinction) and unexpected (biogeography, embryology). It's notable that it is the fossil record that serves as this pivot point, being both a source of potentially powerful objections to evolutionary theory and home to some of its most compelling new explanations. In this chapter, I present both sets of arguments, and consider what role Darwin gave to fossil evidence, in the process attempting to discover why it might have played this unique role in two different parts of Darwin's "long argument" for evolution by natural selection. Geology's special place, I argue, derives from its particular importance in Darwin's social and intellectual context.

Darwin famously described the *Origin of Species* as "one long argument" (Darwin 1859, 459), and that argument reaches a crucial turning point in the ninth and tenth chapters. As the project has often been reconstructed, by a variety of commentators (Hodge 1977; 1989; 1992; Lennox 2005; Hull 2009; Lewens 2009; Waters 2009; Pence 2018), a first phase establishes the existence of natural selection by analogy with artificial selection as practiced by agricultural or horticultural breeders; a second phase proposes that natural selection – given the much longer time that it has to act and its ability to work on invisible characters as well as the visible characters on which breeders might focus – could indeed be capable of producing the kinds of adaptations we see around us in the natural world, and (equally importantly) that it can resist the

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various objections that one might raise against it; and third, and lastly, a kind of responsibility or consilience phase, in which Darwin contends that a whole host of biological cases that might be inexplicable or at least confusing in the absence of evolutionary theory are provided simple and clear explanations in light of evolution by natural selection.

When we see the argument as a whole in this way, Darwin's treatment of the fossil record in chapters nine and ten sits squarely between the second and third parts of the program. On the one hand, the fossil record poses a significant challenge to natural selection. If there really has been a gradual evolution of every existing living form, then the fossil record should be full of myriad transitional forms marking the history of every evolutionary change: the manifold gradations between dinosaur and bird, or between whales and their terrestrial ancestors. The absence of such fossil evidence is, at least *prima facie*, a refutation of a gradual theory of evolution. But on the other hand, the fossil record is a perfect example of the kind of power that an evolutionary framework can give us. Explanations of extinction, of the resemblances between living and fossil groups, of the slow and steady rate of change of organisms over time, and more are all to be found in the geological record.

Darwin recognizes the peril that this presents to his nascent theory. "He who rejects these views on the nature of the geological record," he writes, "will rightly reject my whole theory" (Darwin 1859, 342). But in doing so such a critic would renounce geology's explanatory power, the beautifully straightforward way in which "all the other great leading facts in palæontology seem to me simply to follow on the theory of descent with modification through natural selection" (Darwin 1859, 343). In this sense, the geological record takes on a double importance in Darwin's work. A reader of Darwin's day would likely have left these two chapters with the feeling either that the objections had been surmounted and the novel explanations were enlightening, or that the theory was unsupported by the fossil record, and thus the proffered explanations were misleading at best. A pivotal moment in the argument, indeed.

Darwin's Geological Sources and Context

A key target in teaching and learning about the nature of science is the social context in which it develops. Darwin, just as any other scientist (as the other chapters in this volume also make clear), was a creature of his time – and his context was that of mid-nineteenth century life and earth science (though there is healthy debate surrounding the relative importance of the different elements of this context; see Richards and Ruse 2016). Geology and (the comparatively new discipline of) paleontology were particularly crucial in this regard. Darwin left for his pivotal voyage on the *H.M.S. Beagle* carrying the first volume of Charles Lyell's *Principles of Geology*, and received the next two volumes by post

at various stops during the trip (Bowler 1989, 157). He regularly cited it – including throughout these chapters of the *Origin* – as having fundamentally shaped much of his thinking about the history of the earth and of the development of life. It's worthwhile, then, to investigate Lyell's approach and to see what imprints it left upon Darwin's presentation.

Lyell's own work, in turn, is a product of a number of influences. First is what has come to be known as the *uniformitarian* theory in geology, perhaps now best exemplified by the work of the late-eighteenth century Scottish geologist James Hutton (though most commonly, at the time, through the summary of Hutton's work by John Playfair 1802; Rudwick 1998, 4). According to all such theories, we should seek no great floods or massive upheavals in order to explain the earth's geological past (*contra*, that is, the approach of the opposing position of *catastrophism*, personified by Lyell's own mentor, William Buckland). Rather, the very causes that we see producing geological change around us today – things like volcanic eruptions, erosion, earthquakes, and so on – are sufficient, when extended over a longer history of the earth, to explain the events detailed in geological record.

This appeal to history sets up what M.J.S. Rudwick has identified as the second major important element of context for Lyell: the idea that the current state of the Earth should be read as the product of the series of contingent events that make up its history. This idea has an intellectual legacy which runs far deeper than I have space to do justice to in a short chapter such as this one.² While this could be seen as having some affinity with the uniformitarian model – after all, the uniformitarian posits a physical history for the Earth as well – an emphasis on the uniqueness of these events gives it a decidedly catastrophist flavor. The version of this view that Lyell received from Buckland would have emphasized the extent to which the historical Earth had been a radically *different* place from the Earth of today, manipulated by different kinds of geological causes (like the Biblical Flood, which Buckland hoped to explain and verify geologically) and (*contra* Hutton, who had written in a time before the discovery and widespread appreciation of extinction) different kinds of living species. But Lyell would leave this catastrophist model behind, and, Rudwick persuasively argues, “what eventually convinced him that the geological deluge was a chimera was the cumulative weight of specific empirical cases, in which the phenomena could be still better explained without recourse to any recent catastrophe” (Rudwick 1998, 5).

Thus Lyell's *Principles* became the manifesto for a renewed uniformitarian system – a uniformitarianism more radical than Hutton's, on which not only the *kinds* of causes acting in geology remain the same over

2 At the very least, landmarks for this view prior to Lyell's work include Buffon's *Histoire naturelle* (1749; for an especially illuminating analysis of the biological context, see Sloan 1987) and the anatomical works of Georges Cuvier (1817; Rudwick 1997).

geologic time, but even their *intensity* has been constant deep into the Earth's past (Cannon 1976). As the young Darwin sets out on the *Beagle* voyage, he immediately goes about explaining the environment around him in a Lyellian vein (Hodge 1983, 13–16), looking, for instance, for explanations of extinction and the fossil record that are generally consistent with Lyell's paradigm (Darwin 1835b). While Darwin the biologist might be read as maturing by a series of divergences from his mentor on the question of species creation and extinction (Pence 2022, 2–6), Darwin the geologist stayed a relatively devout Lyellian for the rest of his career.

Darwin is therefore approaching his study of geology with a quite rich social and intellectual heritage, a heritage that was the object of dispute and the subject of transition during this period. To take one illustrative example, consider one of Darwin's personal mentors, the geologist Adam Sedgwick, whose "geology walks" may well have inspired some of the examples that Darwin would later use in these very chapters (Darwin 1958, 69–71; Secord 1991). Sedgwick would remain, throughout his career, an opponent of uniformitarianism, and in fact would, for lack of empirical evidence, become increasingly skeptical of general geological theories as a whole, whether they be uniformitarian or catastrophist (Barrett 1974, 149–50). He was, on the one hand, instrumental in the development of Darwin's reputation as a professional scientist, having communicated some of Darwin's early results from South America to the Geological Society and thus assured his reputation upon his return from the voyage (Darwin 1835a), but, on the other, a staunch opponent of his former student's theory of evolution (Sedgwick 1860).

Just after Darwin's return from the *Beagle* voyage, Lyell, as president of the Geological Society, elected Darwin its secretary. He and Lyell would remain fairly regular correspondents for decades. Darwin's first major professional role within the scientific community, then – as evidenced by these interactions with Sedgwick and Lyell, and his membership in the Geological Society – was as a geologist. These relationships can be extremely illuminating for a broader perspective on Darwin's intellectual milieu (Manier 1978), especially in the early years of his career as he was initially crafting the theory of evolution. First, we see clearly the extent to which the hard and fast divisions between scientific disciplines with which we are familiar today were simply absent in the nineteenth century. It was not in the slightest unusual for Darwin to be professionally respected both as a geologist and as a naturalist, a member of the Geological Society who is nonetheless not often remembered today for his geological writings. As James Secord notes, "it is easy to forget that the most extraordinary decision he ever made was to devote his life to the study of the natural world by becoming a geologist" (Secord 1991, 133).

More generally, this period of five years, from Darwin's return to London in 1837 until his departure for his home in Down in 1842 and

subsequent life as a somewhat reclusive rural man of science, marked the peak of Darwin's daily social engagement as an active, highly connected, prolific (or perhaps better, overworked) member of the British scientific community. It is not easy even to survey the theoretical developments that Darwin undertook during these years, which included much of the early construction of natural selection in his notebooks (Hodge 2009) – but in any case, a constant throughout the entire period was his extensive personal and practical engagement with geology, inside and outside the environs of the Geological Society. In an important sense, then, natural selection was born in a thoroughly geological context. After he left London, his social and professional context changed radically – as Rudwick notes, he ceased being involved in geological fieldwork, published in geology only the remaining studies from the *Beagle* voyage, and was much less influential at the Geological Society (Rudwick 1985, 458). But the mark of geology had already been stamped on the theory of natural selection.

Taming the Fossil-Record Objection

Nonetheless, evolution constituted a relatively dramatic break with the geologists to whom Darwin had turned for inspiration. Even a staunch uniformitarian like Lyell had made room in his theory for the special, divine creation of living beings, and he remained skeptical of and cautious about, though not at all hostile to, evolution by natural selection (Lyell 1863, 407–21; Rudwick 1998, 13). In the ninth chapter of the *Origin*, Darwin canvasses a number of the objections to his new theory which might be raised on geological grounds, objections with which he was all too familiar.

First and foremost is simply the vast amount of time that seemed to be required for evolution by natural selection to produce the degree of diversity that we see in the living world. For all that Lyell's theory had tried to radically extend our horizon for a “plausible” age of the Earth, Darwin's incessant emphasis on the *slow* and *gradual* character of the changes in natural selection seemed to mean that even the vast period of time that Lyell required for geological change would not suffice for the development of life in a Darwinian manner. Darwin readily saw that being able to come to grips, even intuitively, with the passage of this much time would be a challenge for many of his readers, just as it was for Darwin himself. “The consideration of these facts,” he noted, “impresses my mind almost in the same manner as does the vain endeavour to grapple with the idea of eternity” (Darwin 1859, 285).

In one of the few numerical calculations present in the entirety of the *Origin*, Darwin derives the amount of time that it must have taken for the denudation of the Weald, a major geologic feature in southwest England with which he was personally familiar, and estimates this to be around three hundred million years. While today's assessment would cut this value roughly

in half, this figure would immediately become the target of intense criticism. William Thomson (later to become Lord Kelvin) would calculate, following from thermodynamic models postulating an Earth that had begun its life as a single molten mass of rock, cooled in the vacuum of space, that the Earth could be no more than around four hundred million years old (Thomson 1862) – apparently insufficient for an extremely gradual theory of evolution by natural selection to take place.³ Darwin was thus quite right to be worried that his assumptions about the age of the Earth would prove hard to swallow, and he could only go so far toward assuaging these worries in the *Origin*.

Setting aside the question of the overall age of the Earth, we can turn to the content of the fossil record itself. First, Darwin launches a lengthy argument to the effect that the fossil record must necessarily be of a lower quality than we might have predicted by superficially surveying our current collections. From a nature of science perspective, it is interesting to note that in support of his larger, theoretical goals, Darwin needs to actually *dispute* the quality of a certain kind of evidence – here, the completeness of the fossil record. There can be very good reasons, at least occasionally, for scientists to question the accuracy, precision, or completeness of established scientific evidence.

In essence, Darwin is contending that there are a host of conditions that need to be met in order for a fossil to wind up excavated, acquired, and cataloged in the collections of paleontologists. Especially in the nineteenth century, only a small area of the world had been carefully surveyed for fossils – largely Europe and a few portions of North America. For the sake of argument, let's assume that we have thoroughly explored the fossils present in these regions that have so far been the focus of paleontological efforts (a fairly implausible assertion). It would still be the case, Darwin claims, that fossils would have been deposited in these areas only for a small fraction of the history of the Earth, as the physical conditions for fossil production are relatively rare. Darwin points out that effectively only in places where large layers of sediment are being deposited (particularly, then, in areas undergoing sea-floor subsidence) should we expect significant fossilization to take place. There will thus be massive temporal gaps between apparently adjacent geological strata – a fact which, he notes, is confirmed by comparative geological studies across Europe, which find certain layers to be “missing” in some areas.

Now, let's assume both that the fossils in a given area have been well explored, and that some of the conditions for fossilization were present in that area. Even this might not be enough to provide detailed evidence of transitional forms. For that, we would need the process of fossil accumulation

³ He would later revise the estimate down by around a factor of ten, making the problem that much worse for Darwin (Kelvin 1895).

to be in action, constantly, for a period longer than the time that it takes for the species in question to diverge. Again, given how committed Darwin is to the slow and gradual action of evolution by natural selection, he thinks that this will be unlikely – it would imply that a very precise set of conditions remained operative, in the same place, for much longer than we have any right to expect. And even in the presence of optimal conditions in an optimally explored area, we might need to look across different strata to find evidence of transitional forms – in which case it would become progressively harder for us to recognize that we were actually looking at the particular common ancestor or transitional form for which we were searching.

In spite of all of these difficulties, Darwin notes that we have nonetheless been surprisingly successful at discovering more and more diverse fossilized forms. Darwin outlines a number of pronouncements from the paleontological literature insisting that a particular form hasn't been or could never be found, and observes that often, within a relatively short time after those assertions are published, the fossil in question is unearthed after all. For instance, Darwin notes that a number of claims to the discovery of the oldest known form of life had been successively revised, finding simpler and simpler forms in lower and lower strata. This success has continued into the modern day; particularly striking is the example of the fossil *Tiktaalik*, a proto-tetrapod species that was discovered by, essentially, a targeted search of geological regions that would be likely to yield rock formations of the relevant age (Daeschler, Shubin, and Jenkins 2006).

Finally, Darwin also picks up, in chapter 9, a more general potential difficulty with evolutionary theory that is all too familiar from today's classrooms. If we ask whether or not transitional forms exist in the fossil record, we have to remember just what it is that we might mean by a transitional form in the first place. "I have found it difficult," Darwin writes, "when looking at any two species, to avoid picturing to myself, forms *directly* intermediate between them" (Darwin 1859, 280). Of course, this is a natural tendency: because we don't know what the common ancestor of two organisms might have looked like (nor, at a quick glance at the descendants, can we tell how long ago it might have lived), it is all too easy to forget that common ancestors will almost certainly not resemble some kind of "average" between two existing organisms. It is thus the case that even if we were in possession of the very fossil specimen that was the common ancestor of two extant groups, we might be incapable of recognizing its importance.

Darwin summarizes his response to all of these potential objections by developing a metaphor for the evidential quality (or lack thereof) of the geological record that is worth quoting at length:

For my part...I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect; of this history

we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. Each word of the slowly-changing language, in which the history is supposed to be written, being more or less different in the interrupted succession of chapters, may represent the apparently abruptly changed forms of life, entombed in our consecutive, but widely separated, formations. On this view, the difficulties above discussed are greatly diminished, or even disappear. (Darwin 1859, 310–11)

Geology in Evolution's Service

With that, then, we move from the ninth to the tenth chapter – from geology as a source of objections and problems to geology as a way in which we might confirm evolution's action, using evolution as a source for new, unexpected, and powerful explanations of the history of life. There is, to be sure, something of a paradox here, underscored by the long quote above. Darwin has just spent a chapter explaining to us the manifold ways in which the geological record might fail to give us a precise picture of the history of life on Earth. To turn around and use this same evidence to ground compelling explanations that will offer support for evolutionary theory will thus require sophisticated and careful argument.

Two particularly striking features of the fossil record, Darwin argues, can be readily explained by evolution (and can only be explained with difficulty from a non-evolutionary perspective). First is the structure of resemblances between fossils. Fossil groups tend to be intermediate in character between living groups, with fossils recapitulating the kind of “group-within-group” structure familiar from Linnaean taxonomy. This makes perfect sense, of course, if those intermediate groups are actually ancestral to living species. Darwin will proceed to construct a similar argument that evolutionary theory offers an explanation for taxonomic classification itself in chapter 13 of the *Origin*. Darwin writes that these group resemblances offer us, “in short, such evidence of the slow and scarcely sensible mutation of specific forms, as we have a just right to expect to find” (Darwin 1859, 336).

Only slightly less important is evolution's explanation of extinction. For Lyell, as Darwin will discuss in more detail in chapter 11, extinction was explained by the redistribution of climatic conditions across the surface of the globe. One could still be a consistent uniformitarian in saying that, while the nature and intensity of the causes of geological change remain the same over time, their distribution across the Earth could differ, thus causing the extinction of species no longer capable of living in their former habitats (Lyell 1832, 129–30). Darwin agreed, but thought that this could only tell part of the story – for he believed that he had seen cases on the *Beagle* voyage of

extinctions without any corresponding change in climatic conditions (Hodge 1983, 21–22).

As Darwin notes, extinction would also follow as a straightforward consequence of natural selection. If the organic world really is as finely balanced as Darwin's invocations of the struggle for life seem to argue, then the slightest change to the relationships between organisms or environmental conditions will likely cause some groups to be favored and others disadvantaged, "and the consequent extinction of less-favoured forms almost inevitably follows" (Darwin 1859, 320). Darwin's understanding of species as the product of common descent with modification also explains the fact that extinction is permanent. Once a species has disappeared, even if another similar species were to arise, it would not be the same species – once the "link of generation has been broken" (Darwin 1859, 344), a group cannot be recovered.

A number of other, smaller features of the geological record are also explicable by evolution. We find in this chapter Darwin's mature view on the concept of *progress*. A question that had haunted him throughout his writings (see, e.g., Ruse 1996, 145–54), Darwin struggled with the tension between the apparent progress toward "higher" organization over the history of life (with human beings at the pinnacle) and the implication of his theory that there was no way in which to derive a global tendency toward a "goal" or "direction" in evolution. Natural selection offers us, at best, a kind of local or piecemeal progress, with descendant organisms having had some kind of advantage that enabled them to spread – but with no guarantee that those advantages would "accumulate" in any particular way. This would still produce something that resembles progress, but it will be progress of a strange sort. "I do not doubt," as Darwin puts it, "that this process of improvement has affected in a marked and sensible manner the organisation of the more recent and victorious forms of life, in comparison with the ancient and beaten forms; but I can see no way of testing this sort of progress" (Darwin 1859, 337). While we might thus expect that today's organisms would outcompete those of the past – they have, after all, accumulated different advantages that let them survive while others perished – there would be no way, in general, to say in advance what form that success might take, and thus no guiding, overall notion of improvement or progress.

Lastly, with the exception of a handful of "living fossil" species, the fossil record gives us extensive evidence of the slow but constant modification of organisms over the course of time. More precisely, it shows us that while almost all organisms are constantly changing, those rates of change are themselves variable, with some groups known to vary faster and others more slowly. This is, Darwin notes, entirely explicable on an evolutionary basis, but difficult to explain if we think that this variability is some kind of intrinsic

feature of organisms or species. A group that is faced with more diverse interactions (whether with other organisms or a more complex environment) will have a more diverse collection of selective pressures to which to respond, and by extension more opportunities for specialization, division of labor, and the other processes that Darwin thinks are crucial for driving speciation.

Geology and the Argument of the *Origin*

It is interesting to note that the fossil record is one of the only facets of the *Origin's* “long argument” that plays both the roles of generator of objections and generator of positive evidence. In that sense, the transition that I noted above from the second, objection-refuting portion to the third, consilience-building part of the book, which takes place between chapters nine and ten, could easily pass without notice. But its significance should not be understated. Darwin often lamented that he was too hemmed in by the constant pressure to respond to objections. As he wrote to his friend and colleague John Stevens Henslow, in response to Sedgwick’s scathing review of the *Origin*, if it was permissible “(& a great step) to invent the undulatory theory of Light—ie hypothetical undulations in a hypothetical substance the ether,” he saw no reason why he could not be permitted to “invent hypothesis of natural selection... & try whether this hypothesis of natural selection does not explain (as I think it does) a large number of facts in geographical distribution—geological succession—classification—morphology, embryology &c. &c.” (Darwin 1860). Darwin’s two chapters on geology thus also encapsulate the ambivalence that he felt, torn between the apparent requirement to respond to all his objectors and his desire to focus on the exciting, fruitful consequences of an evolutionary world-view.⁴

The importance of these two chapters of the *Origin* comes as no surprise. The fossil record has been and remains a crucial source of evidence, dispute and debate with regard to evolutionary theory. It is likely the first thing that a new student of evolutionary biology would think of when asked to identify the base of evidence that supports an evolutionary explanation of the history of life. As Darwin makes apparent, however, the relevance of this evidence to the phenomena, or the relationship between evolutionary theory and the fossil record, is much more complex than it might at first appear. Many of the obvious, most simplistic inferences that we might draw – like the idea that we will confirm evolutionary theory in every lineage, just by tracing out

4 The idea that Darwin’s responses to objections cloud the force of his argument has often motivated philosophers of biology to read the first edition of the *Origin*, prior to the integration of many such responses. The opinion goes at least as far back as Darwin’s son Leonard, who wrote to R. A. Fisher that he wondered whether “it would be worth republishing the *first* edition of the *Origin of Species*...because it was written before my father had been subject to *any criticism whatever*” (L. Darwin to Fisher, [late-September 1926?], Bennett 1983, 81, original emphasis).

the history of transitional forms between two groups of interest – will not only be falsified (there are many groups for which this will be impossible), but would even serve as objections to the coherence of evolutionary theory itself (in the absence of such sequences of transitional forms, why not reject the evolutionary explanation outright?). The ways in which the fossil evidence supports evolution must thus be selectively and cautiously argued. Darwin clearly saw this double-edged role for geology in evolution and embraced it, making it a central part of the argument of the *Origin*.

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