

Evolution in Fossil Lineages: Paleontology and *The Origin of Species*

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ABSTRACT: Of all of the sources of evidence for evolution by natural selection, perhaps the most problematic for Darwin was the geological record of organic change. In response to the absence of species-level transformations in the fossil record, Darwin argued that the fossil record was too incomplete, too biased, and too poorly known to provide strong evidence against his theory. Here, this view of the fossil record is evaluated in light of 150 years of subsequent paleontological research. Although Darwin's assessment of the completeness and resolution of fossiliferous rocks was in several ways astute, today the fossil record is much better explored, documented, and understood than it was in 1859. In particular, a reasonably large set of studies tracing evolutionary trajectories within species can now be brought to bear on Darwin's expectation of gradual change driven by natural selection. An unusually high-resolution sequence of stickleback-bearing strata records the transformation of this lineage via natural selection. This adaptive trajectory is qualitatively consistent with Darwin's prediction, but it occurred much more rapidly than he would have guessed: almost all of the directional change was completed within 1,000 generations. In most geological sequences, this change would be too rapid to resolve. The accumulated fossil record at more typical paleontological scales (10^4 – 10^6 years) reveals evolutionary changes that are rarely directional and net rates of change that are perhaps surprisingly slow, two findings that are in agreement with the punctuated-equilibrium model. Finally, Darwin's view of the broader history of life is reviewed briefly, with a focus on competition-mediated extinction and recent paleontological and phylogenetic attempts to assess diversity dependence in evolutionary dynamics.

Keywords: fossil record, Charles Darwin, modes of evolution, stasis, gradualism, diversity dependence.

Introduction

Why then is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely-graduated organic chain; and this, perhaps, is the most obvious and serious objection which can be urged against the theory. (Darwin 1859, p. 280)

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Passing from these difficulties, all the other great leading facts in palaeontology seem to me simply to follow on the theory of descent with modification through natural selection. (Darwin 1859, p. 343)

In *The Origin of Species*, Charles Darwin presents two different views of the fossil record that are relevant to his proposal for descent with modification via the mechanism of natural selection. First and most prominently, he was deeply troubled by the lack of stratigraphic sequences that recorded the gradual transformation of one species into another, a phenomenon he felt was a necessary prediction of his theory (first quote above). The title of chapter 9, “On the Imperfection of the Geological Record,” gives away Darwin's resolution of this apparent contradiction: the fossil record, he argues, is far too incomplete to document evolutionary sequences in detail, and therefore it offers no forceful objection to evolution by natural selection. In the second area of his engagement with the fossil record, Darwin steps back from individual lineages to view the fossil record as an archive of the broader history of life. At this coarser scale, Darwin suggests that paleontology is pleasingly consistent with evolution by natural selection (second quote above).

My goal here is to reevaluate Darwin's claims about the relevance of paleontology for understanding evolutionary processes in light of what is known now, 150 years later, about the nature and content of the geological record. The pace of paleontological research has been rapid and accelerating, and I cannot meaningfully review all of the ways in which the fossil record bears on evolutionary understanding. Rather, the scope here is more limited to *The Origin of Species* and the claims made therein regarding paleontological evidence. Darwin's interest in the transformation of species was intense, and his treatment of this topic was extended. In contrast, his discussion about the broader history of life was more selective, drawing, as it must, from the rather limited information available at that time about large-scale paleontological patterns. This two-part structure and relative emphasis will be followed in this article.

The Transformation of Species

Darwin's explanation for the lack of gradual fossil transitions relies on his interpretation of the geological record as being woefully incomplete. In this section, I consider Darwin's interpretation of the geological record before I assess what the cumulative paleontological evidence has to say about the nature of evolutionary changes within lineages. Although the influence of Darwin's commitment to gradual change was long lasting, for much of the twentieth century the data to assess changes in fossil lineages were fragmentary and inadequate. Most of the relevant evidence we have today was not collected until the model of punctuated equilibrium (Eldredge and Gould 1972) challenged the notion of geologically gradual change and revived interest in the nature of species-level evolutionary transitions.

The Quality of the Fossil Record

That our palaeontological collections are very imperfect, is admitted by every one. (Darwin 1859, p. 287)

Now turn to our richest geological museums, and what a paltry display we behold! (Darwin 1859, p. 287)

Of most critical interest to Darwin was that "mystery of mysteries," the origin and transformation of species. For the fossil record to inform about this subject, Darwin realized that it must be relatively complete over the time-scales in which species evolve. Lacking reliable means of absolute dating, he was not explicit about the durations of time involved,¹ although below I will argue that it is possible to calibrate his scenarios to geological time. Nevertheless, Darwin argued forcefully that the geological record was insufficient to trace the detailed evolutionary trajectories of lineages. Specifically, he noted that paleontological samples were often small and fossils were often fragmentary; that fossils had been collected from only a small part of the world; that unmineralized remains are unlikely to fossilize and even hard parts are worn down and destroyed when unburied; that entire habitats are poorly represented in collections; that the periods of time between preserved geological formations were often vast, and within formations, sediment accumulation was intermittent and shorter overall than the duration of species transformation; and that spatial shifts in geographic ranges of species can obscure their recorded histories (Darwin 1859, p. 287–302).

¹ Darwin's calculation of time in excess of 300 million years for the erosion of the Weald, a set of Mesozoic strata in England, was widely criticized, and he omitted it in the third and subsequent editions of *The Origin of Species* (Burchfield 1974).

Darwin's comments on the poverty of the known fossil record reflected, in part, the state of geology as a young field. In the mid-nineteenth century, systematic documentation of the stratigraphic record had been ongoing for only a few decades (Rupke 1983; Rudwick 1985). Although some of Darwin's geological contemporaries held more optimistic views of geological completeness (see Foote 2010), it is nevertheless true that fossils were known mostly in the few areas in which early geologists were located. As an example, consider the fossil record of dinosaurs (fig. 1). Worldwide, it consisted of only 56 occurrences in 1859, almost all of which were in Europe and mostly restricted to Great Britain. These data were downloaded from the Paleobiology Database (<http://paleodb.org>), which for dinosaurs is heavily indebted to the synthesis and compilation of Carrano (2008). Each occurrence represents the collection of a fossil currently recognized as a dinosaur, and these occurrences sample about 23 unique dinosaur species (M. Carrano, personal communication in January 2010). Thus, when Darwin laments the paltry holdings of paleontological collections and the primitive state of knowledge about the fossil record, he does so with good reason.

This concern, while operative in 1859, has much less force today. In the past 150 years, paleontologists have collected an enormous number of fossils, and these fossils have been integrated into a vastly better-understood geological framework. Dinosaurs, which were barely known in 1859, are now represented by over 9,000 occurrences in the Paleobiology Database (fig. 1). This contrast actually underestimates the increase in paleontological collections because, in the mid-nineteenth century, almost every fossil find would be novel and thus would be reported. Today, repeated finds of well-known taxa from standard localities are much less likely to find their way into the published literature that is the source of the Paleobiology Database. Although dinosaurs have a generally spotty fossil record, they are useful for this comparison because of a concerted effort to vet, evaluate, and input into the Paleobiology Database their occurrences, especially for the oldest historical finds (Carrano 2008).

Darwin's observations about bias and completeness would today mostly fall under the heading of taphonomy, which is the study of the processes of preservation and their effects on the information present in the paleontological record (Behrensmeyer et al. 2000). In many respects, Darwin's views on the shortcomings of the fossil record are still credible today, and some of his concerns about preservation bias and geological incompleteness merit extensive treatment in modern overviews (Kidwell and Flessa 1996; Martin 1999; Behrensmeyer et al. 2000; Holland 2000; Kidwell and Holland 2002). There are indeed usually large temporal gaps separating preserved geo-

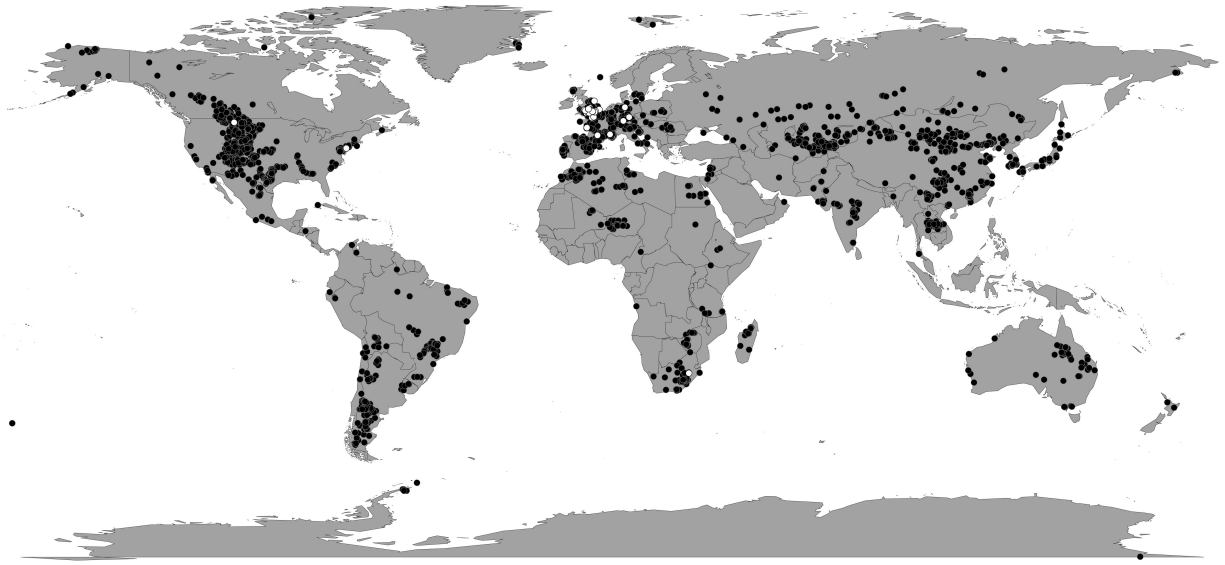


Figure 1: World map showing the 9,076 occurrences of dinosaurs in the Paleobiology Database. The 56 occurrences known as of 1859 are indicated by open circles; all other occurrences are indicated by filled circles. Footprint and dinosaur egg taxa are excluded; these data, especially those from 1859, rely heavily on the compilation by Carrano (2008).

logical units (Peters 2006) and between individual beds within units (Kowalewski and Bambach 2003); in terms of strict temporal completeness, the fossil record is very often more gap than record. In addition, stratigraphic completeness is inversely related to temporal resolution (Sadler 1981). Thus, at coarse temporal resolution, a particular stratigraphic section may be perfectly complete in that each large temporal bin is represented by at least some preserved sediment. When time is divided more finely for the same section, however, most of these finer temporal bins may not be represented by any rock; at this finer temporal scale, this hypothetical section would be very incomplete (see, e.g., Peters 2008). This scale dependence of completeness confirms Darwin's intuition that the fossil record can be informative at broad scales but may not be adequate for addressing processes occurring at finer resolutions. Moreover, fine temporal divisions within a locality are often impossible to correlate between localities and regions, limiting the degree to which geographically integrated observations can be temporally resolved.

Another factor, little known to Darwin, further compromises the ability of paleontologists to resolve time. In most settings, paleontological samples represent accumulations that are time averaged over many biological generations. This occurs because sedimentation is usually slow relative to biological production and because sediments can be mixed by storms and waves and by organisms via burrowing and other activities (a subject that would later engage Darwin through his work on earthworms).

Durations of time averaging vary greatly across taxa and sedimentary environments, but they commonly exceed 10^3 years and can occasionally be much longer (Kidwell and Behrensmeier 1993). For example, in marine shallow-shelf environments, direct dating of shells lying on the surface of the seafloor routinely yields ages of hundreds to thousands of years (Flessa et al. 1993; Kowalewski and Bambach 2003). Although this temporal mixing can be advantageous because it filters short-term variability (Olszewski 1999), it has a negative consequences for inferring evolutionary patterns. By summing over temporally separate populations, time averaging essentially collapses evolutionary differences between generations into variation within samples, with a resultant loss of resolution.

This time averaging should inflate phenotypic variances in fossil samples, but its magnitude will depend on the severity of temporal mixing and on the pace and nature of evolutionary changes (Bush et al. 2002; Hunt 2004*b*). Studies comparing variance in modern populations with that in time-averaged fossil samples have found surprisingly little evidence for variance inflation (Bell et al. 1987; MacFadden 1989; Bush et al. 2002), and a quantitative survey indicated that even substantial time averaging increases phenotypic variance by an average of only about 5% (Hunt 2004*a*). This finding suggests that evolutionary changes over 10^3 – 10^4 years must often be quite modest, an observation that anticipates the discussion of stasis below.

Darwin's concerns about some kinds of heterogeneity

in the fossil record, while undoubtedly valid, are less critical for the goal of tracing evolution within lineages. It is true that jellyfishes, like most animals lacking mineralized skeletons, do not have a rich fossil record. And some habitats, such as the rocky intertidal zone (of interest to Darwin because of his studies on barnacles), are dominated by erosion more than by sedimentation and so have poor preservation potential. However, these considerations are not fatal; they only force restrictions in scope to taxa with durable skeletons living in readily preserved habitats. While we will likely never have a detailed knowledge of changes in fossil jellyfish lineages, this is no barrier to documenting evolution in taxa that are well represented in the fossil record. In fact, recent research suggests that the sedimentary records of groups such as mollusks and mammals can be very faithful to original biological signals (Kidwell 2001; Lockwood and Chastant 2006; Western and Behrensmeyer 2009).

Modern paleontologists can also extract much more useful information from the same rocks than could the paleontologists of Darwin's day. This is particularly true for dating the ages of fossil-bearing strata. Radiometric dating of geological materials was unavailable until the early twentieth century (Dalrymple 1991), and these methods have become much more precise in recent years (Ogg et al. 2008). Moreover, a wealth of new tools can be used to determine relative ages and correlations among rocks preserved in different areas (e.g., Harries 2003) and to infer environmental conditions from geochemical properties of fossils and sediments. The fossils themselves also convey more information than they used to. Our understanding of the biology of extinct organisms is better, and repeated rounds of discovery and analysis have resulted in much-improved awareness of the phylogenetic relationships among extinct and extant taxa.

One of the most important limitations facing Darwin was that he had to infer phenotypic change qualitatively by noting when paleontologists documented the replacement of one named species or variety with another through a stratigraphic section. Especially over the past 40 years or so, this taxonomic approach has been supplanted by biometric analyses. Because of these efforts, we now have a reasonably large pool of studies featuring carefully measured morphology within inferred ancestor-to-descendant sequences of populations, at least at temporal resolutions typical for the fossil record (10^4 – 10^6 years; fig. 2).

It is certainly true, as Darwin noted, that the fossil record is incomplete. But in science, information is always incomplete, and so it is more important to know whether the fossil record is adequate for addressing a particular question (Paul 1982; Kidwell and Holland 2002). In the face of an imperfect fossil record, two general approaches may be employed to understand phenotypic evolution

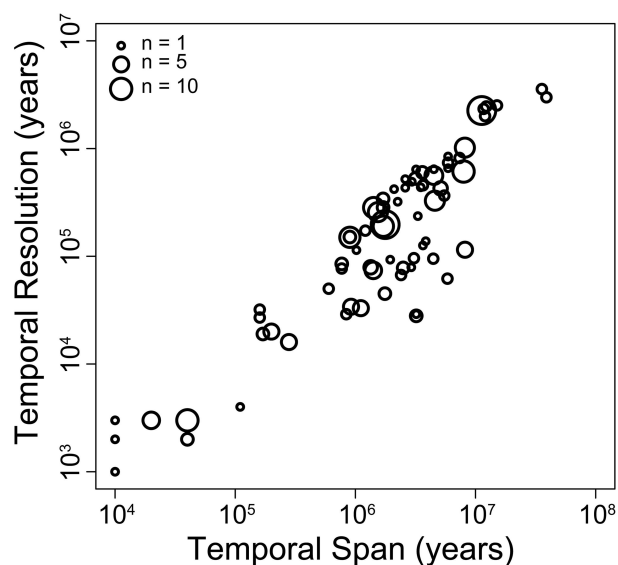


Figure 2: Temporal resolutions (median intersample duration) and temporal spans (total duration from first to last sample) for 251 documented evolutionary sequences of trait values from Hunt (2007*b*). This compilation includes multiple traits measured from the same set of samples; circle size is proportional to the number of sequences with the same resolution and duration plotted together (key in upper left corner).

within lineages. First, one can focus on the most promising cases so that, to the greatest extent possible, all the normal shortcomings and biases of the fossil record do not interfere. Second, one can consider fossil evidence more broadly, weighing the more numerous examples while being mindful of their nature and limitations. In the next two subsections, I take each of these approaches in turn.

A Best Case

Darwin saw natural selection as the most important mechanism by which species change. Especially since the contributions of Simpson (1944) to the Modern Synthesis, paleontologists have mostly agreed with this idea, and patterns in the fossil record have been interpreted routinely in terms of adaptive evolution. Actually demonstrating the role of natural selection, however, has turned out to be surprisingly difficult. Toward this goal, several methods were developed using neutral genetic drift as a null hypothesis (Lande 1976; Turelli et al. 1988; Lynch 1990). The expectation was that bouts of adaptive evolution could be detectable as faster-than-drift evolution. Application of these tests, however, almost always yielded paleontological rates that were slower than the neutral expectation (Lynch 1990; Cheetham and Jackson 1995; Clegg et al. 2002; Estes and Arnold 2007; Hunt 2007*a*), an unexpected finding that did not clearly support or refute the claim that the

evolutionary changes documented by paleontologists are driven by natural selection.

A remarkably favorable case study for documenting the transformation of a fossil species via natural selection involves skeletal armor reduction in a lineage of stickleback fish from a 10-million-year-old lake in Nevada (Bell et al. 2006). Here preservation is excellent, and fossil fish are numerous and articulated. Most unusually, sediments in this ancient lake were deposited in undisturbed yearly layers called varves. Thus, in principle, time in this environment can be resolved to individual years. In practice, fish are not so abundant in each varve as to allow meaningful analysis, and so specimens were lumped into 250-year temporal bins. Even with this lumping, the temporal resolution of this system is outstanding compared with what is usually attainable in the paleontological record.

In addition to these promising geological circumstances, there are good biological reasons to favor natural selection in explaining the observed evolutionary trajectories of decreasing armor (fig. 3). Research on modern stickleback populations has shown that reduced armor can evolve rapidly when predatory fish are rare or when water chemistry is unfavorable for bone deposition (Bell et al. 1993, 2006; Reimchen 1994). Fossils of predatory fish are extremely rare in these deposits, and there is evidence of repeated evolution of reduced armor morphology in this ancient lake basin. Moreover, multiple armor-related traits, all of which are likely to have been genetically independent, evolved in parallel. All of these lines of evidence

suggest that the observed evolution of these traits was governed by natural selection (Bell et al. 2006; Bell 2009).

These qualitative considerations can be evaluated by fitting to these data an explicit model of adaptive evolution (Hunt et al. 2008). The specific model used is that of a population located some phenotypic distance from an optimal morphology. In this scenario, the evolutionary approach to the optimum is initially rapid, but then it tapers according to what is called an Ornstein-Uhlenbeck process (Lande 1976; Hansen 1997). The derivation of this model assumes constant and ample standing variation, but a general decelerating approach to an optimum holds even when evolution occurs through the fixation of new mutations (Orr 1998). This model makes particular sense here because the initial population in figure 3 is inferred to mark the initial colonization of the paleolake, which might be expected to differ in selective conditions from the ancestral habitat of this lineage. Moreover, this adaptive model provides an excellent fit to these data (fig. 3, *dashed line*), and one that is decisively better than that for neutral drift (Hunt et al. 2008). This advantage in support for the adaptive model implies that selection actually favored phenotypes with reduced skeletal armor, as opposed to the scenario in which selective constraints are absent when predation is low. The fitness benefit for the low-armor form may follow from energetic and growth-rate costs of secreting bone in low-ion freshwater environments (Marchinko and Schluter 2007).

The adaptive model considered here is simple in that it

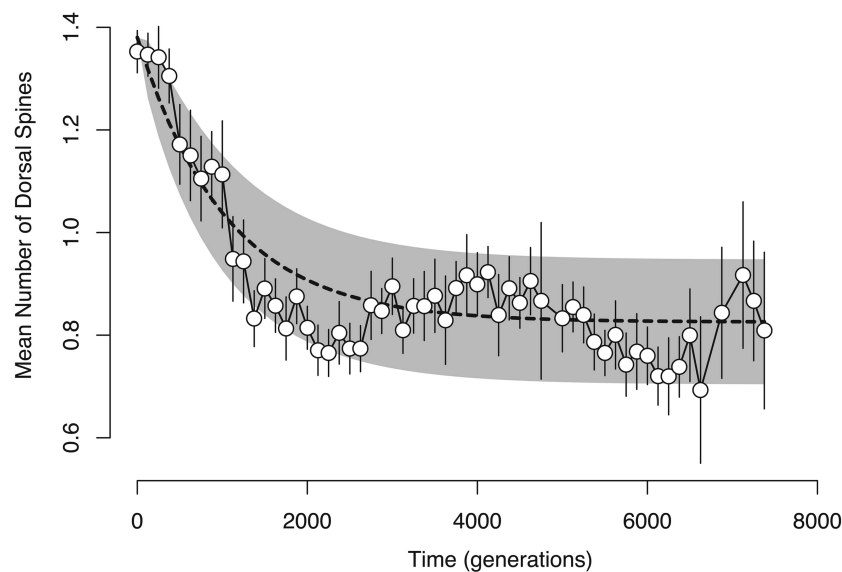


Figure 3: Evolutionary trajectory in a lineage of stickleback fish from an ancient lake deposit. Each circle represents the average number of dorsal spines (one aspect of skeletal armor) over intervals of approximately 250 years. The dashed line shows the expected evolutionary trajectory for the best-fit adaptive model, and the gray area is the 95% probability interval for the fit.

assumes that the position of the optimum does not change over the interval. Of course, this assumption may not hold, and some of the deviations from the expected trajectory may be attributable to variation in selective conditions (e.g., when values are lower than expected around generation 1,500 and higher than expected near generation 4,000). However, in finite populations, genetic drift should also cause meandering deviations, and it may be difficult to discriminate between these possibilities without additional information. One could fit additional models that assume temporal variation in the optimum, which would help to evaluate plausible limits on variability in the position of the selective peak. In addition, we can predict that if the deviations from the expectation are caused by variation in selection for armor development, then they should be present in all three skeletal measurements made for this stickleback lineage. We should therefore see parallel deviations in all three skeletal traits, but no such concordance is apparent (see Hunt et al. 2008; fig. 1).

In fact, the extent of meandering deviations can be used to compute an independent consistency check on this adaptive model. The magnitude of excursions around the expectation reflects the potency of drift and thus the effective population size (N_e). In very large populations, drift is negligible and populations will hardly deviate from the expected trajectory. In small populations, drift will produce much larger excursions (Lande 1976). The magnitude of variation around the expectation can be converted to an estimate of N_e under the assumption of a fixed adaptive optimum (see Hunt et al. 2008). For the three traits measured by Bell and colleagues (2006), estimates of N_e are compatible across traits and are reasonable for populations of lake stickleback (approximately 600–6,000, depending on trait heritabilities). Because the N_e calculations are independent across traits, this consistency need not occur, and therefore it provides some reassurance that the model fit reflects biological reality (Hunt et al. 2008).

For this very best case scenario, we can observe what Darwin hoped the fossil record would reveal: the step-by-step transformation of a lineage through natural selection. The mathematical form of this trajectory was not available to Darwin, but the qualitative picture is concordant with his views. Nevertheless, this example also suggests some pessimism about capturing adaptive trajectories in the fossil record. Parameter estimates from the model fit suggest that natural selection on these armor traits was weak (the strength of selection can be computed from the rapidity of the approach to the optimum: stronger selection results in faster convergence; Lande 1976; Arnold et al. 2001). From the observed stickleback trajectories, the fitness difference between the starting phenotype and the adaptive optimum is approximately 1% (Hunt et al. 2008). Even with this very modest difference, almost all of the strongly

directional change is completed within about 1,000 generations. It is only the exceptional resolution afforded by these varved sediments that allows the adaptive evolutionary pattern to be discerned. Under conditions more typical for the paleontological record, the smooth tapering trajectory would degrade to a single pulsed shift, instantaneous at coarser geological resolution. As discussed in the next section, this speed of change likely would have surprised Darwin, and it serves as an important guide for thinking about what evolution by natural selection ought to look like in the fossil record.

The Fossil Record of Lineage Evolution: A Broader Survey An Expectation of Gradual Change.

Although each formation may mark a very long lapse of years, each perhaps is short compared with the period requisite to change one species into another. (Darwin 1859, p. 293)

Given the limited paleontological collections available at the time, Darwin was justified in arguing that the known paleontological record did not contradict evolution by natural selection. We now have much more data on evolving fossil lineages, but it is not exactly straightforward to compare this emerging picture with Darwin's views. This is partly because *The Origin of Species* is a rich document. Many passages emphasize the slow and gradual nature of changes within lineages, but some acknowledge that patterns could also be more complex. A passage inserted into later editions acknowledges that rates of evolution could be quite variable and perhaps often quite low (Darwin 1872, p. 279; see Gould 1982, p. 84). Regardless, Darwin's qualitative descriptions of rate are not easily converted to real units that may be compared with fossil data.

There is one specific claim that can be used to calibrate to absolute time the pace of change as envisioned by Darwin. He suggested that one reason for the lack of transitional forms is that fossiliferous formations record periods of time that are much shorter than the great lengths of time involved in the transformation of one species into another (quote above). Because formations last on the order of a few million years (with roughly an order of magnitude in variation; S. Peters, personal communication in June 2009), we can convert Darwin's suggestion into the very testable notion that the time to transform one species into another is typically more than a few million years. Thus, Darwin's view makes an important prediction: as paleontologists amass more and more data-tracing lineages over timescales from hundreds of thousands to millions of years, an increasing number of species transformations will be revealed. This prediction became an expectation, at least among many paleontologists. For example, although Simpson (1944) was keenly aware that

evolution could be very rapid, nevertheless he still judged directional, gradual evolutionary trajectories to be well represented in the fossil record. This assumption of geologically gradual change was challenged by Eldredge and Gould (1972), who argued that the traditional expectation of steady evolutionary divergence over millions of years—what they called phyletic gradualism—was fundamentally incorrect as a description of the empirical fossil record. Instead, they suggested that most species exhibit stasis, or little net change over time, with evolutionary changes concentrated into punctuations associated with lineage splitting. The linkage between speciation and pulses of morphological change was not read directly from the fossil record, but instead it was seen as a consequence of allopatric speciation.

Eldredge and Gould's (1972) punctuated-equilibrium model was controversial with two different constituencies, for different reasons. Among population geneticists (Charlesworth et al. 1982), punctuated equilibrium was suspect because it invoked nonstandard mechanisms for both punctuation and stasis that hinged on the establishment and breakdown of genetic constraints (Eldredge and Gould 1972; Gould 1982). In general, these suggestions about mechanism have not fared well, and when punctuated equilibrium has been advanced in the recent literature it has generally been done with more standard neo-Darwinian processes such as variation, selection, and gene flow (Lieberman and Dudgeon 1996; Gould 2002; Eldredge et al. 2005; Geary 2009), although substantial differences of opinion remain about the relative importance of these mechanisms. Quite separately, some paleontologists criticized punctuated equilibrium, calling it an inaccurate description of paleontological patterns (see, e.g., Gould and Eldredge 1977; Gingerich 1985 and references therein). This disagreement spurred competing interpretations of evolutionary trajectories, with gradualists emphasizing the continuity of change and punctationalists focusing on variation in rates from slow (stasis) to fast (punctuations). At the time, there was no means for deciding which of several competing interpretations was best supported by data, and in this sense the debate could not be resolved.

Determining microevolutionary mechanism is often difficult with fossils, and I consider briefly a few aspects of this issue in a later section. Questions of pattern should be much easier, however, and next I assess whether the aggregate fossil record of lineage evolution supports Darwin's prediction of gradual change or whether it reveals the pulses and stasis of punctuated equilibrium.

The Relative Dominance of Different Evolutionary Modes. In part because of the subjectivity involved in interpreting evolutionary patterns, published overviews ar-

rived at incompatible conclusions about the relative importance of gradual change versus stasis and punctuation in fossil lineages (Gingerich 1985; Erwin and Anstey 1995; Jackson and Cheetham 1999; Levinton 2001; Gould 2002). These disagreements persisted despite the fact that the overviews considered a largely overlapping set of paleontological case studies. This was clearly an unsatisfying state of affairs, and a series of statistical procedures were developed to help recognize different patterns, or modes of evolution² (Raup 1977; Raup and Crick 1981; Bookstein 1987; Gingerich 1993; Roopnarine 2001). These studies settled on three canonical modes of change: directional evolution, random walk, and stasis. The first of these can be equated with Darwin's expected pattern of gradual change during the transformation of species. Stasis was originally defined rather broadly to encompass most patterns lacking strong directionality, but usage was later narrowed to describe patterns in which morphology showed minimal fluctuations around a stable mean. A random walk is a simple model in which evolutionary increments are independent and trait increases and decreases are equally probable. Like stasis, it is not inherently directional. But, unlike stasis, random walks actually go somewhere and produce increasing evolutionary divergence over time.

Random walks were key to the statistical methods that were developed because they were used as null models. They were given null status because they were seen as the simplest possible notion of evolution consistent with ancestor-descendant dependence (Bookstein 1987). Moreover, among the three modes, only the random walk was specified as an explicit statistical model that could serve as a null hypothesis. The shortcoming of this strategy was that these tests had low power to reject the null hypothesis of a random walk (Roopnarine et al. 1999; Sheets and Mitchell 2001), and so their application was not always very informative. This limitation can be overcome by employing a different statistical approach. Rather than designating a null hypothesis, each mode can be expressed as an explicit statistical model and fitted to data via maximum likelihood (Hunt 2006). Models can then be compared on equal footing using the Akaike Information Criterion (AIC) or related metrics that measure support in a way that weighs both goodness of fit and model complexity. Examples of empirical fossil sequences that are best fitted by directional evolution, random walk, and stasis are presented in figure 4.

This statistical approach creates an avenue for resolving

² The term "modes of evolution" descends from Simpson (1944), and it has become standard when referring to qualitatively distinct patterns of change in fossil lineages. In this context, "modes" does not refer to the population genetic mechanisms of evolution (selection, drift, mutation, gene flow).

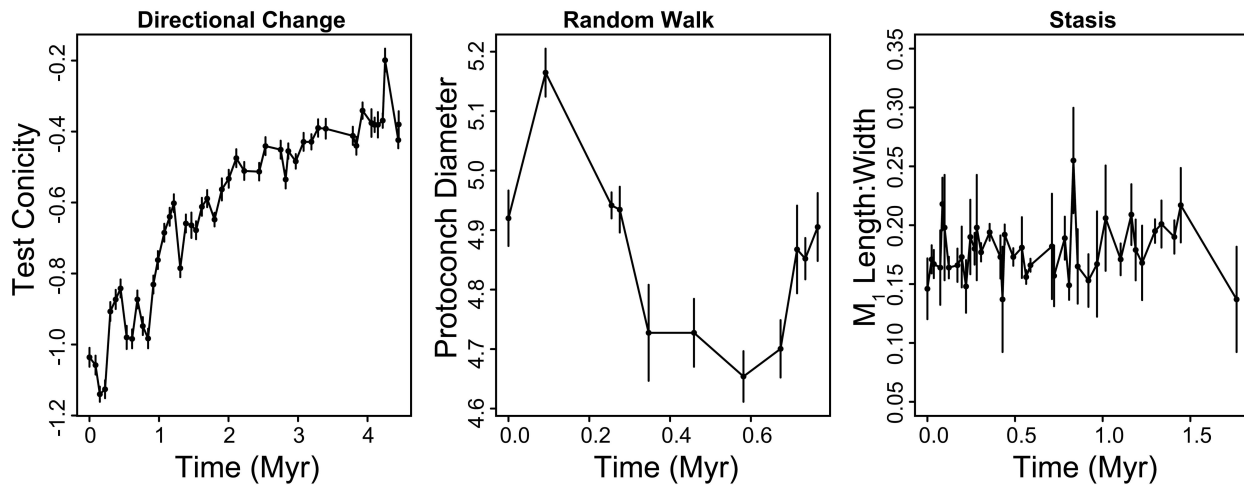


Figure 4: Examples of evolutionary sequences from fossil lineages that represent the three canonical modes of evolution, as indicated by the small-sample-size Akaike Information Criterion. *Left*, directional change in test shape from the planktonic foraminifera *Contusotruncana* (Kucera and Malmgren 1998); *center*, a random walk in protoconch diameter from the benthic foraminifera *Discocyclina* (Fermont 1982); *right*, stasis in the length-to-width ratio of the lower first molar of the mammal *Cantius* (Clyde and Gingerich 1994). Each point represents a sample mean; error bars indicate 1 SE. Time is in millions of years elapsed from the start of the sequence.

the debate about the preponderance of evolutionary patterns within lineages: simply fit the three modes of evolution to all available case studies and tally how often each model is the best supported of the three. This procedure found that gradual, directional change was the best-supported model in only 5% of 251 cases examined, with the remaining 95% split approximately equally between random walks and stasis (Hunt 2007*b*). This finding supports a key claim of punctuated equilibrium: directional evolution is rarely observed on paleontological timescales. This does not mean that directional evolutionary changes are rare; more likely, they are usually too brief to be resolved in the geological record. This conclusion is consistent with the best-case stickleback example discussed earlier and the extensive documentation of rapid evolution in living populations (Hendry and Kinnison 1999).

Punctuations. Directional evolution, random walks, and stasis are homogenous models in that the rules governing change are assumed not to change during an evolutionary sequence. This uniformity assumption can be relaxed in a variety of ways. Because of punctuated equilibrium, the violations of homogeneity that have been of most interest are those that imply pulsed change. Typically, punctuations are envisioned as a three-stage model in which a lineage experiences first stasis and then rapid directional change, followed by a return to stasis. This model can be incorporated readily into the likelihood framework, although the details of implementation differ, depending on the rapidity of the pulsed change relative to the temporal spac-

ing of the samples (Hunt 2008). Models with punctuations and other heterogeneities are more complex than the homogenous modes discussed above, but their greater number of parameters can be accounted for when models are evaluated using the AIC. An example for which a model

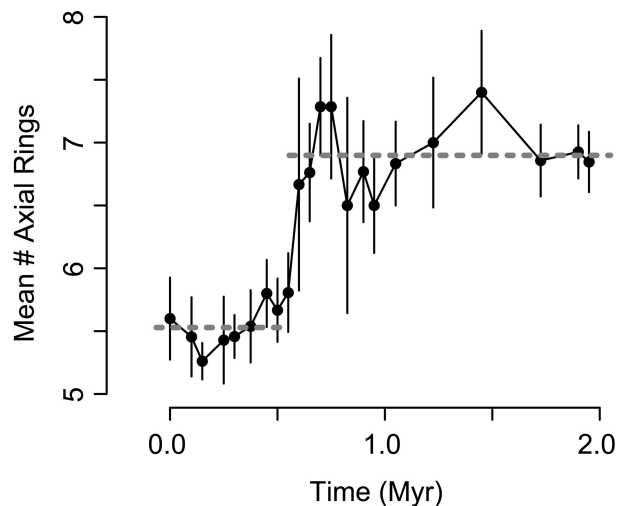


Figure 5: Evolution of the number of axial rings in the pygidium (posterior body region) of a trilobite lineage in the genus *Flexicalymene* (Cisne et al. 1980). This sequence is best fitted by a model with a single, punctuated change occurring after the ninth sample (Hunt 2008). Dashed lines show the phenotypic values for the intervals of stasis before and after the punctuation; plotting conventions otherwise are as for figure 4.

with a rapid punctuation is better supported than all uniform models is shown in figure 5.

Within-lineage patterns were dissected and disputed as to whether they exhibited pulsed change and were thereby consistent (or not) with punctuated equilibrium. This focus on within-lineage patterns may seem slightly curious, given that Eldredge and Gould (1972) argued specifically that bursts of change were associated with lineage splitting. Accordingly, it may not be clear whether punctuations not associated with speciation support, refute, or even relate to punctuated equilibrium. This shift in emphasis to within-lineage punctuations was practical because only a few studies (e.g., Lazarus 1986) have potentially sampled splitting events in the fossil record.

It is exactly because speciation is so elusive—too slow to observe in the present day, too rapid to capture in the geological record—that better tests of punctuated equilibrium rely on clades rather than isolated lineages. Several different articles have summarized these studies, although not necessarily from the same perspective (Erwin and Anstey 1995; Levinton 2001; Gould 2002). Of the case studies commonly reviewed, the work of Alan Cheetham and colleagues (Cheetham 1986, 1987; Jackson and Cheetham 1990, 1994; Cheetham and Jackson 1995) on cheilostome bryozoans from the Caribbean Neogene is widely regarded as coming closest to the ideal system with which to evaluate the central claims of punctuated equilibrium. In addition to good stratigraphic sampling and careful morphometric design, this work used extant species to confirm the genetic distinctiveness of morphospecies and to estimate trait heritabilities. This suite of studies revealed patterns of phenotypic change that were in agreement with the central predictions of punctuated equilibrium: through their histories, species changed very little relative to morphological distances between ancestor and descendant lineages. In addition, ancestral species routinely persisted after the establishment of descendant species, a pattern that is inconsistent with the anagenetic transformation of entire lineages.

However, even in this nearly best case, the relationship between lineage splitting and morphological punctuations is still somewhat uncertain because fossil species are recognizable as separate entities only if they are morphologically distinct. Therefore, it may be difficult to discriminate punctuated equilibrium from a scenario in which phenotypic changes are pulsed but not coincident with lineage splitting. Phylogenetic methods that assess the relationship between speciation events and morphological divergence within clades of extant species can potentially help to resolve this impasse (Bokma 2002, 2008; Ricklefs 2004, 2006; Monroe and Bokma 2009), but accounting for speciations that are erased by subsequent extinction is a challenge (Bokma 2008). Moreover, these approaches rely on simple

models of morphological change to infer punctuations, and the performance of these methods is unknown under more realistic scenarios. There are viable biological mechanisms that link phenotypic divergence to lineage splitting (Futuyma 1987; Schluter 2000, 2001), but uncertainty remains over the pervasiveness of this link. Ideally, more direct evidence of the link between cladogenesis and morphological evolution would follow from studies of the phylogeography and paleontology of populations, species, and clades merged to produce a time-space integrated view of phenotypic divergence.

Natural Selection and Paleontological Patterns. How do these evolutionary modes relate back to the process of natural selection envisioned by Darwin? Perhaps unsurprisingly, the relationship between paleontological patterns observed over millions of years and generation-to-generation microevolution is complex. One can write out equations for expected evolutionary change over long periods of time, given a model of selection and assumptions about the genetic basis of traits (Arnold et al. 2001; Estes and Arnold 2007). The difficulty lies in the reverse operation, inferring process from pattern, because multiple evolutionary scenarios can produce any specific pattern of paleontological change. For example, take the pattern of stasis. A lineage can fluctuate in morphology because it experiences stabilizing selection around a fixed adaptive optimum, because it tracks an optimum that itself fluctuates over time, or because of more complex scenarios involving selection and gene flow across structured populations, among other possibilities. In situations like the stickleback example described above, in which exceptional temporal resolution and good auxiliary biological information are available, it may be possible to infer specific microevolutionary processes. Under more typical circumstances, I am less optimistic about this possibility. Thus, while the three canonical modes of evolutionary change are all consistent with natural selection acting in some capacity, none can be attributed unambiguously to any single microevolutionary scenario.

However, the main contribution of patterns of evolution in fossil lineages is not elucidating microevolutionary processes. The mechanisms of population genetics are presumably complete, but they do not constrain how evolutionary changes should unfold over millions of years. Should they be gradual or pulsed? Should changes be associated with speciation? Should divergence be unbounded or proscribed by narrow adaptive limits? Because population genetics is consistent with all of these possibilities, it cannot discriminate among them (Ayala 1982, 2005). Exploring patterns of change within fossil lineages provides traction in addressing these and other questions that are

crucial for a richer understanding of the evolutionary dynamics of lineages and clades.

The Broader Fossil Record

Whereas Darwin was deeply distressed about the fossil record's lack of detailed species-level transitions, he found much in the broader fossil record to support his views. He cited multiple lines of paleontological evidence that support the common ancestry of organisms. Darwin noted that formations often yielded taxa that were morphologically intermediate between those of overlying and underlying formations and that extinct forms sometimes filled morphological gaps between living taxa. In addition, he argued that clades generally expanded and declined incrementally, rather than all at once. He amassed these observations in favor of a shared history among lineages and in opposition to special creation (Darwin 1859, p. 315) and catastrophism (Darwin 1859, p. 316–317). The paleontological documentation for morphological transitions between major groups of organisms has, of course, become much more impressive in the intervening century and a half (Prothero 2007).

That species descend from other species is no longer scientifically controversial, and so Darwin's arguments in favor of this idea are not of great interest here. Similarly, I will not review Darwin's suggestion that the trend of increasing complexity many paleontologists observed in the fossil record could be reconciled with the mechanism of natural selection. Complexity is a difficult concept to operationalize, especially when dealing with fossils, and existing treatments of the subject already dissect the conceptual difficulties of studying complexity and review much of the relevant paleontological evidence (McShea 1994, 1998). Instead, I will focus this section on Darwin's suggestion of a link between competition and the origin and extinction of taxa. This issue is timely in that it resides at the intersection of recent paleontological and biological inquiries about the evolutionary dynamics of clades.

Dynamics of Clades: Origination, Extinction, and Competition

On the theory of natural selection the extinction of old forms and the production of new and improved forms are intimately connected together. (Darwin 1859, p. 317)

Although Darwin acknowledged that organisms face diverse biotic and physical challenges, competition was central to his view of the fates of individuals and lineages (Paterson 2005). This focus is apparent in his discussions of extinction, which he strongly linked to the origin of new species. Because new lineages are formed in the cru-

cible of competitive interactions, Darwin thought it usual that they would be equipped with some advantage over preexisting forms, which they would then displace in the struggle for existence. Close relatives of new forms would suffer disproportionately from this outcome because they would share most ecological traits with the new and improved lineages. Origination thus begets extinction, placing a negative feedback on diversity.

The idea that ecological overlap should be most severe among close relatives is consistent with functional traits having high heritability at the species level (Jablonski 1987) or, equivalently, high phylogenetic signals (Freckleton et al. 2002; Blomberg et al. 2003). This notion touches on many paleontological issues, ranging from the persistence of ancestors to controls on global diversity. In the following sections, I will review briefly some of these strands, starting at the finest phylogenetic scale and moving outward from there.

Descendants Displace Ancestors.

Hence the improved and modified descendants of a species will generally cause the extermination of the parent-species ... (Darwin 1859, p. 321)

There is no phylogenetic relationship closer than that of ancestor and descendant. It therefore might be supposed that their competitive interactions may be particularly intense and, if Darwin is correct, that improved descendants may often drive their ancestral forms to extinction. Given a fossil record that preserves ancestors and their descendants, this claim is paleontologically testable. In practice, implementing such tests is a challenge. They require a fossil record that is rather complete to allow for the routine preservation of direct ancestors (Foote 1996), as well as a reliable means of actually recognizing ancestor-descendant relationships, an endeavor some scientists believe to be problematic (e.g., Engelmann and Wiley 1974).

Pearson (1998) tested Darwin's suggestion that descendants outcompete their ancestors to extinction, by using the fossil record of several ocean-dwelling plankton groups (foraminifera, nannofossils, and graptoloids). The ancestor-descendant calls in this study derive from traditional phylogenetic interpretations by microfossil specialists. These are made without recourse to explicit algorithms, and instead they rely on a relatively literal reading of the fossil record that clusters specimens into lineages and clades on the basis of morphological similarity and stratigraphic position. More sophisticated means of identifying ancestors and descendants exist (Fisher 1994; Smith 1994; Marcot and Fox 2008), but the traditional approach is reasonable for character-poor but richly preserved taxa such as planktonic microfossils.

For each inferred speciation, Pearson traced ancestral

and descendant species to determine which became extinct first. In each of the five data sets, ancestors preferentially became extinct before their descendants, consistent with Darwin's notion of competitive replacement. This analysis implicitly assumed that extinction risk does not change with taxon age, an assumption that may be violated for planktonic foraminifera (Doran et al. 2006). Nevertheless, simple tests suggest that this effect does not account for the preferential extinction of ancestors (Pearson 1998). It is worth noting that the inference of competition is indirect in that it is based solely on the temporal ranges of species; no ecological information is considered. If Darwin's notion of descendants outcompeting ancestors to extinction truly occurs, then this result should hold disproportionately when ancestor and descendant species have the most ecological and geographic overlap. Testing this prediction would more fully assess the linkage between these stratigraphic patterns and competitive interactions.

Diversity-Dependent Diversification. Moving phylogenetically outward, the same argument about competitive displacement applies to taxa with close but collateral relationships, such as congeneric species. This kind of a dynamic offers an intrinsic brake on diversification, and Darwin clearly did not envision a world in which diversity increases without bound (Darwin 1859, p. 320). This dependence of diversification rate on standing diversity can occur when speciation rates decrease or extinction rates increase with increasing numbers of taxa, leading to clades with quasi-stable diversities (Rabosky 2009a). Recent methodological advances have spurred interest in this issue by allowing inference of diversification histories from molecular phylogenies of extant taxa (Pybus and Harvey 2000; Rabosky and Lovette 2008a, 2008b). These methods often produce a signal of decreasing diversification over the lifetime of a clade (McPeck 2008; Phillimore and Price 2008; Reznick and Ricklefs 2009). This pattern is usually interpreted in terms of niche-filling models in which successful speciation becomes less probable over time as the available adaptive space becomes occupied within an ecological and geographic context (Phillimore and Price 2008; Rabosky 2009b; Reznick and Ricklefs 2009).

Paleontologists have investigated diversity dependence more directly by estimating standing diversity, speciation rates, and extinction rates over multiple intervals in the geologic past. Quantitative analyses support diversity dependence for the entire marine invertebrate fossil record over the Phanerozoic (Alroy 2008; Foote 2010), for coarse divisions thereof (Sepkoski 1978, 1979, 1984; Foote 2000; but see Stanley 2007), and for large groups of mollusks (Miller and Sepkoski 1988; Wagner 1995). Evidence for diversity dependence in fossil mammals appears to depend on the analytical protocols used (Alroy 1996, 1998, 2009).

In addition to the analyses specifically designed to test for diversity dependence, the fact that origination and net diversification rates are elevated after the most severe extinctions (Alroy 2008; Krug et al. 2009) also suggests an influence of diversity on extinction and/or origination.

Although paleontological and phylogenetic approaches share the goal of uncovering the diversity dependence of clade dynamics, there are substantial difficulties in integrating these two kinds of studies because they are usually performed at vastly different temporal and phylogenetic scales. Paleontological studies commonly span hundreds of millions of years, include hundreds to thousands of taxa, and consider genera as the unit of diversity. In contrast, phylogenetic analyses focus on species composing small to medium-sized clades of geologically recent origin. For example, the phylogenetic studies included in the meta-analysis of bird clades by Phillimore and Price (2008) cover a median age of less than 10 million years and a median richness of less than 50 species. This compares with Alroy's (2008) study of the fossil record of over 18,000 marine invertebrate genera spanning 500 million years. Differences in scope can be bridged from both directions through phylogenetic analyses of very large clades (e.g., Smith and Beaulieu 2009) and paleontological efforts that separately analyze clades rather than entire faunas (e.g., Stanley 2007). Differences in phylogenetic resolution (species vs. genera) are more problematic, as large paleontological studies are challenging to complete at the species level because, relative to higher taxa, species have stratigraphic ranges that are more incomplete and they are more difficult to recognize consistently across time and space. However, such studies are invaluable for linking to modern phylogenetic analyses, and every effort should be made to cultivate these high-quality data sets.

Even if paleontological and neontological approaches can be integrated and diversity dependence can be demonstrated, challenges remain in relating such patterns to the scenario of competition-mediated extinction envisioned by Darwin. One problem is that although Darwin hypothesized diversity-driven extinction, diversity dependence may arise from the dynamics of speciation more than from extinction (Gilinsky and Bambach 1987; Alroy 1998; Phillimore and Price 2008; Rabosky and Lovette 2008b; Quental and Marshall 2009; Foote 2010). Moreover, linking patterns that are manifest in whole faunas over many millions of years, all the way down to competitive interactions among close relatives, is not straightforward (Jablonski 2008), especially given the time resolution and completeness constraints inherent in the fossil record. One key to discriminating causal mechanisms will be to integrate studies of phylogenetic topology and stratigraphic ranges with explicit analysis of the ecological attributes of taxa (Sepkoski et al. 2000; McPeck 2008; Rabosky 2009c).

More broadly, Darwin clearly saw competition and other biotic interactions as more important than abiotic circumstances in determining the ultimate fates of species. The relative importance of these two classes of factors is a persistent theme in paleontology (Allmon and Ross 1990; Barnosky 2001; Benton 2009). While some visions agree with Darwin in giving primacy to biotic interactions (Van Valen 1973; Vermeij 1987; Hubbell 2001), on the whole, paleontologists probably place greater emphasis on changes in the physical environment. This focus may result, at least in part, because of the clear geological and chemical signatures left by physical perturbations such as climate change (Cronin 1999), asteroid impact (Alvarez et al. 1980), and changes in ocean circulation (Erbacher et al. 2001), to name just a few. Biotic interactions, in contrast, leave discernible traces in only a few circumstances (e.g., McKinney 1995; Kelley and Hansen 1996; Kowalewski et al. 1998; Gahn and Baumiller 2003). Thus, while competition obviously operates in nature, how it shapes the long-term history of lineages and clades is difficult to assess (Jablonski 2008; Benton 2009), and a fair reckoning of the determinants of extinction will also include substantial contributions from incumbency and physical perturbation (Rosenzweig and McCord 1991; Jablonski 2008).

Conclusion

The Origin of Species is perhaps the greatest example of an approach to science in which all possible lines of evidence, no matter how disparate, are brought to bear on a central issue. Darwin wove together observations from many fields of biology (taxonomy, behavior, development, biogeography, and plant and animal breeding, among others) and from subjects more distant, including geology. Darwin concluded that whereas the broad outline of the fossil history of life was consistent with descent with modification and natural selection, the geological record was too incomplete and too poorly known to document in detail the transformation of species.

One hundred and fifty years later, we are in a different position. The fossil record is much better known, and its strengths and weaknesses are much better understood. Under the most promising circumstances, it is possible to document in fossil strata the transformation of a lineage by natural selection as Darwin envisioned, although he underestimated the speed at which such changes occur. We also now have a good quantitative record of evolutionary patterns in fossil lineages over typical paleontological resolutions (10^4 – 10^7 years). At these scales, phenotypic evolution within lineages appears to be overwhelmingly nondirectional and often surprisingly slow. The meandering and fluctuating trajectories captured in the fossil record are not inconsistent with the centrality of

natural selection as an evolutionary mechanism, but they probably would not have been predicted without the benefit of an empirical fossil record. In addition to providing a record of phenotypic evolution, paleontology testifies to the ubiquity of extinction and provides a means to test proposed explanations for its causes. Darwin's favored explanation of competition-mediated extinction can be evaluated and compared with proposals that rely on other drivers, including physical perturbations.

Still, we are not as close as one would like to realizing Darwin's vision of an integrated understanding of evolution. Even estimates of the same quantities, such as speciation and extinction rates, are difficult to compare between paleontological and biological studies because of the discrepancies in phylogenetic and temporal scales. There are practical reasons for these and other differences, but they are not insurmountable. One methodological key will be to harness simple models that can be used equally in paleontological and phylogenetic contexts. For phenotypic evolution, simple models like random walks (or Brownian motion) make predictions about the distribution of traits both in ancestor-descendant sequences and across the tips of phylogenies. Model fits and parameter estimates can address evolutionary questions across paleontological and biological studies. Similarly, birth-death models confer probabilities on the occurrences and stratigraphic ranges of taxa, as well as on branching times in a phylogeny of extant species. Each source of evolutionary information has its own strengths and limitations. For example, phylogeny and ecology are more accessible in the present day than they were in the distant past, but extinctions are much more difficult to constrain in the absence of fossil data. If we are to follow Darwin's lead and make progress toward a synthetic understanding of the evolution of species, a necessary priority will be to develop tools and data sets that permit full integration of observations from the fossil record with those from the living biota.

Acknowledgments

I thank D. Schemske for organizing and inviting me to participate in the Vice President's symposium. I am grateful to R. Bambach and D. Erwin for their help with the history of geology, to S. Peters for advice on durations of geological formations, and to M. Carrano for guidance on dinosaur occurrences in the Paleobiology Database. C. Marshall, K. Roy, and D. Schemske provided thoughtful comments that improved the manuscript. I acknowledge the Paleobiology Database as the source for figure 1; my thanks to all those responsible for inputting those dinosaur data.

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Symposium Editor: Douglas W. Schemske