

A Paleontological Look at History

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The fossil record of animal life is far more incomplete and patchy than even the most obscure historical records. Consequently, some of the approaches developed by paleobiologists over the past couple of decades to assess the reliability of the fossil record, investigate patterns and infer underlying processes may be useful in analyzing historical data as well. Here I discuss two examples where paleontologists have investigated historical questions, in one case the evolution of cornets, in the second estimating the survival rate of Medieval manuscripts. Depending on the scope of big history, there are a number of areas where history and paleontology overlap, particularly in the investigation of early human history. More rigorous analysis of the biases of the historical record may be of some use in determining which historical patterns are sufficiently reliable for further exploration.

Introduction

Paleontology, astronomy, geology and archaeology and aspects of evolutionary biology are historical sciences. They differ fundamentally in their approach and methods from largely ahistorical disciplines as physics, chemistry, physiology and much of molecular biology [5, 21, 25]. Physicists often assert that because they are not predictive, historical sciences are no more sciences than history. Such assertions commit at least two errors.

The first is to ignore the vastly greater number of potential variables in historical disciplines than in physics, with an attendant increase in the complexity of interactions between them (physics is predictive because its subject matter is relatively simple). Complex dynamics make a mockery of prediction, as evidenced by the lack of reliable climate and earthquake forecasts (see discussion by Krakauer, this volume). But not even the most arrogant physicist (perhaps a redundant class) would doubt that the study of climate and earthquakes is scientific.

The second logical error is that of uniformitarianism (also known as actualism). Physicists *assume* (the proof is more difficult) that their underlying laws are constant through time and space. They are not perplexed by the possibility that the speed of light or the nature of the neutrino was different 2.5 billion years ago or on the other side of the Universe. In historical disciplines the uniformitarian assumption is far less reliable and often demonstrably false. Indeed a promising question to explore in many historical sciences is how

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historical processes change through time. True, the historical sciences have less recourse to direct experiment, and their evidence may often be fragmentary or missing. Yet the historical sciences have developed a range of statistical and quantitative techniques to assess the reliability of historical data, quantify patterns of change, and develop models of the underlying processes and the more limited use of narrative.

Physicists have a role here, bringing a powerful set of quantitative tools and approaches, particularly in the development of first-order, process-based models. Statistical techniques are hardly unknown in history and have been widely adopted throughout the social sciences. What may be useful in the conversation between historians and scientists is an exploration of some of the approaches developed by paleobiologists over the past couple of decades to assess the reliability of the fossil record, and investigate historical patterns and the inference of underlying processes. Here I also discuss two examples where paleontologists have used such approaches to investigate historical questions, in one case the evolution of cornets, in the second estimating the survival rate of Medieval manuscripts. Depending on the scope of big history, there are a number of areas where history and paleontology overlap, particularly in the investigation of early human history and the conceptual framework discussed here may be of some use as the field expands. Finally, I will explore some of the implications of non-uniformitarian issues in understanding historical disciplines.

The Missing Record

Many of the works of classic antiquity are known only from comments in other classical manuscripts: of the more than 80 plays of Aeschylus, only seven remain; seven of the 120 plays of Sophocles; some 18 of 90 by Euripides and there are works of Pliny and other authors of which there are no known copies. Cisne applied a Markov model of birth and death processes to the probability of survival of manuscripts on arithmetical and calendrical calculations from Late Antiquity and the Middle Ages (Cisne [4]; see comment by Gilman and Glaze [15]). In such a model a manuscript has a probability of being copied (analogous to giving birth in a model of population demography) and being destroyed (analogous to death). Since manuscripts are copied by hand their intrinsic growth rate should be exponential. Cisne shows that the resulting model of the birth and death dynamics of manuscripts is identical to the Verhulst-Pearl logistic equation for population growth, familiar to generations of ecologists. Using data from the number of copies of four of the Venerable Bede's technical works, Cisne shows that their age distribution closely follows age distributions expected for populations with logistic growth. Based on this model Cisne comes to the somewhat surprising conclusion that many, if not most, scientific texts in existence in the early Middle ages are likely to have

survived to today. He suggests that the reason for the demise of copies of Aristotle's missing works, and others from Antiquity is preservational (an issue also familiar to paleontologists): manuscripts on parchment were more like to survive than older ones on papyrus. This is a sharp departure from the more general assumption that the disappearance of manuscripts from Antiquity is simply a function of time. The assumptions in Cisne's models have been criticized [6, 15], but to dismiss the effort would be too harsh, Cisne's work might better be seen as an opening effort in the development of more robust models and assumptions to document patterns of cultural transmission.

Cisne came to the issue of the survival rate of manuscripts from a paleontologists concern with the quality of the fossil record. To a first approximation the record of the history of life is entirely missing. The fossil record reflects the fortuitous preservation and recovery of durably skeletonized, common and often geographically widespread species, usually from the marine realm rather than on land. (To a geologist terrestrial deposits are generally being eroded, and deposited in the oceans, so it is nice when dinosaurs and other land-based organisms are preserved, but it is not the way to bet.) The fossil record may record 1-2% of all the marine animal species that have lived during the 575 million years since the origin of animals, and an even smaller percentage of the plants and animals that have lived on land. Paleontologists have some sources of information of the history of life, including tracks and trails preserved in sediments (trace fossils) and molecular fossils (biomarkers), but the bulk of our knowledge of the history of life is dependent upon the preserved body fossils of now extinct organisms. Moreover, some depositional settings are better at preserving organic remains than others: limestones and shales are, for example, generally better than sandstones. This produces considerable spatial and temporal variability in the quality of the fossil record.

For historians and archaeologists, as for paleontologists, the quality of the record declines the further one goes into the past. For paleontologists this decay in the fidelity of the fossil record means that there are fewer deposits of greater age, it is more difficult to correlate between rocks of similar age as there age increases (a necessary precondition of determining a global pattern), the uncertainties on the age of fossils at a particular locality increase with age, and the quality of preservation generally declines. One consequence of this is that the sorts of questions that we can address necessarily change for older deposits. My colleagues working on the past few million years of time are able to ask, and answer, questions about ecological relationships. Working in rocks 270 or 510 million years old, I can only dream of having similar resolution.

Practitioners of Big History face similar problems, and some of the solutions devised by paleontologists may prove useful. Consider, for example, the issue of the domestication of agriculture. It is exceedingly unlikely that archaeologists have actually recovered the earliest sites where plants or

animals were domesticated, although they have greatly narrowed the geographic region in most of the centers of domestication [3, 42]. Techniques that paleontologists have developed for placing statistical confidence intervals on the first and last appearances of fossil clades based on the frequency of recoveries [24, 30] may prove similarly useful in assessing historical problems.

A critical question for paleontologists is to reconstruct the pattern and eventually the underlying processes of the history of life. With this knowledge in hand, paleontologists can then investigate the significance of changes in the environment, the importance of evolutionary innovations, and what other factors control diversity. The literature in this area is too rich and diverse to address here, so I will confine myself to using a long-standing debate over the record of global marine diversity through the past 600 million years as an example of the issue.

There are many components of diversity, including the variety of form, the range of developmental styles, and the generation of different ecological groupings [10]. Many of these have no ready metrics, so paleontologists have tended to focus on the number of taxa (taxonomic units such as species, genera, or families) over this time. Some paleontologists argued that global diversity had been expanding nearly exponentially since the end-Permian mass extinction 252 million years ago [38, 40], while others suggested that diversity reached a maximum early in the history of animals, perhaps 450 million years ago, and subsequent changes have largely been changing relative frequency, rather than absolute diversity [28, 29]. In the later model lack of sediments and other preservational problems have produced a pattern very different from the “real” one. Resolving the difference between these two end members remains the object of considerable effort, and even if no resolution is yet available, the problems are better understood [36, 37].

Unfortunately, the vagaries of preservation mean that counting fossil species is too subject to error. Instead, paleontologists have agglomerated species into more inclusive units in the Linnean taxonomic hierarchy, generally genera or families (groups of related genera). Sepkoski generated an exhaustive compilation of the first and last occurrences of marine families through the past 600 million years [31-34] and eventually expanded this to marine genera [35]. Although the patterns revealed by Sepkoski’s analysis achieved iconic status, there are a number of potential biases that cloud the results. The first and last occurrences of a taxon are unlikely to represent the actual origin or extinction of the lineage. Statistical tools have been developed to adjust range durations to account for this problem, but doing so requires knowledge of not just the first and last occurrences, but the frequency of occurrences of a taxon near the range endpoints [7, 24, 30]. In the absence of such data global compilations have not been adjusted for this problem. In these analyses Sepkoski was concerned that the more complete sampling of living biotas might artificially extend the ranges of some taxa across intervals

where they are unrecorded from the fossil record. In other words, a genus of fossil crab might only be known up to the late Miocene, 5 million years ago, but is also known from living representatives. Thus the range of the genus extends to today. To adjust for this “Pull of the Recent” he removed all recent taxa and analyzed only the fossil occurrences.

Variations in sampling and collecting intensity produce a related set of problems. Intervals of geologic time with abundant, well-preserved and easily accessible fossiliferous rock in Europe and North America tend to be far better sampled by paleontologists than intervals with more poorly preserved fossils or greater difficulties in access. Fortunately these variations in sampling intensity between regions can be corrected through the use of rarefaction techniques. Rarefaction is a statistical technique to compare samples of different sizes to determine the number of taxa if the same number of specimens had been sampled between the two time intervals [27].

In Sepkoski’s original study he lacked information on how often taxa had been found between their first and last occurrences. For his purposes such information was not critical, but as better datasets were developed (often by his own students), the issue of how to count diversity became more critical. Does one count all the taxa found in an interval? What about taxa found before and after an interval, but not within a specific interval? Should one count only taxa that are found in adjacent intervals (“boundary crossers”) but not those found only within a single interval? Such “singletons may reflect poor taxonomy or other problems These and other problems have led to the generation of a wide range of diversity metrics, and applied to large data sets, they will produce very different patterns of diversity [12, 13]. Recently a group of paleontologists has produced a new picture of marine diversity for the past 600 million years, based on a compilation of diversity from specific localities, rather than just first and last occurrences [1, 2]. This group also used a variety of new statistical methods, including rarefaction and different counting metrics. Their results are considerably different from Sepkoski’s, (Fig. 1) in showing a much smaller increase in marine diversity toward the recent, and a very different pattern of crises and expansions. For example, the apparent exponential increase in diversity over the past 100 million years disappeared, as have some mass extinction events and a rapid increase in diversity beginning about 480 million years ago. In short, this new diversity plot emphasizes very different events than those many paleontologists have spent the past two decades studying. Unfortunately there are problems with this new analysis as well, so paleontologists and evolutionary biologists are even more in the dark about the patterns in the history of life than before.

Here my goal is not to advocate the adoption of specific methods, but rather to show how such a seemingly simple issue as the global diversity over the past 600 million years raises some difficult issues when examined more thoroughly. Since understanding process requires a basic agreement on pattern, this

dispute threatens to paralyze parts of the paleontological research agenda. In the absence of a better understanding of diversity patterns, it is difficult to determine, for example, how climate has influenced diversity [11], or even when major increases have occurred in biodiversity and what environmental circumstances or new adaptations may have facilitated them. Some of these statistical techniques from paleobiology, ecology and evolutionary biology might have relevance for the description of specific historical patterns in big history, and specifically for establishing which “patterns” are sufficiently robust to warrant further study.

Reconstructing Evolutionary Trees

The only figure in Charles Darwin’s *The Origin of Species* is an evolutionary tree, used to illustrate the concept of descent with modification. Darwin’s evolutionary perspective was grafted on to a pre-existing system of systematics developed by Carl Linnaeus, the means of classifying and organizing the relationships between species, genera and more inclusive evolutionary groups. Overall morphologic similarity was often the primary evidence for inferring a relationship between two entities and provided the basis for classification. Since the 1980s, however, systematists have realized that overall similarity is a poor guide to evolutionary relationships, as it fails to distinguish similarity due to descent from a common origin from convergence on a common form for other reasons. New methods of reconstructing these phylogenetic relationships were developed relying on the statistical analysis of large datasets of specific character states. Such techniques have recently been profitably used to explore technological evolution and provide much-needed rigor to historical linguistics [18, 26]. It has also been applied to aspects of cultural evolution [23], although it is not always clear whether the horizontal transmission of cultural information violates the assumptions of vertical transmission embedded within phylogenetic methods.

Although cornets are now similar in form and tone to a small trumpet, they are historically descended from a coiled horn and thus independently derived from trumpets. One question in the evolution of musical instruments is how this transition came about [8]. Temkin and Eldredge applied phylogenetic methods to elucidate this evolutionary transition, coding a matrix from historical collections of cornets. The character matrix was based not on overall similarity of the shape of the cornets, but on specific, discrete characters. The pattern of shared, derived characters defined the patterns of evolutionary descent, and also illuminated horizontal transmission of ideas and technologies between different makers of cornets [39]. But since the historical evolution of cornets is so well documented, Temkin and Eldredge were able to identify areas where the phylogenetic methods failed as well. Such applications of phylogenetic methods are often informative because both biological and

cultural evolution share certain properties of descent with modification. The application of such biological approaches to cultural evolution is also criticized because of the extensive horizontal transmission that occurs in cultural evolution and learning. Yet microbes also happily transfer useful genetic information among quite disparate lineages [16, 43]. The application of comparative phylogenetic methods to the evolution of cultural diversity has been explored [22].

Contingency and Pattern in the History of Life

Properly characterizing the patterns in the history of life is critical for evaluating one of the most divisive issues among paleontologists: the likelihood of regularities governing the history of life. This is an area that cuts to the core of Big History as well, and to the issue of whether one can, in principle, develop a science of history. The late Stephen Jay Gould of Harvard was one of the foremost proponents of the contingency matters school of evolutionary history. Beginning with his book *Wonderful Life* [17], Steve argued that the course of life, and the waxing and waning of different clades (major groups of organisms that share a common line origin, for example mammals) does not reflect adaptive superiority, as pure Darwinian evolutionist might argue, but was often been driven by chance or contingent events. Steve based much of his argument on the fossils of the Burgess Shale, an extraordinary 505 million year old, Middle Cambrian deposit of soft-bodied and lightly skeletonized marine animals. The Burgess Shale reveals animals otherwise unrecorded from the fossil record, including armored onychophorans (think of a short earthworm with legs and spines), and my personal favorite, *Opabinia regalis*, a cousin of arthropods with five eyes (each on its own eye stalk) and a single long proboscis ending in a claw positioned like an elephant's trunk. Steve famously argued that if one could "run the tape of life again" annelids (earthworms and their allies) might be less common than priapulids or arthropods might not be one of the most dominant phyla; perhaps the descendents of *Opabinia* might be among us still.

Sea urchins provide one of my own favorite examples of contingency. Some 270 million years ago there were about seven different genera of sea urchins, but only one or two species survived the great end-Permian mass extinction 252 million years ago, when about 95% of all marine species became extinct [9]. The primary survivor (*Miocidaris keyserlyi*) belonged to a genus with a particular morphology that is shared by all the descendents of this now very diverse and abundant group. One can of course come up with a story, perhaps even a plausible one, about why *Miocidaris* survived the Permian calamity. But any such story is inherently untestable. It is just as likely that its survival was due to luck and nothing more. But if luck it was, the approximately 800 living species of echinoids reflect a far greater array of morphologies, and life habits

than seemed possible before the end-Permian mass extinction. So this contingent event had a tremendous impact on the history of this group, and arguably on the structure of modern marine ecosystems. Steve Gould argued that often events leading to the disappearance of a group could not have been predicted nor could the effect they had on diversity (number of taxa) and abundance (number of individual organisms). If this argument is generally correct then it seems to limit the possibility of identifying general patterns in the history of life.

The alternative argument is that whatever the importance of contingency in individual cases, such as the effect of the 10-kilometer diameter bolide that struck the early 66 million years ago, the general trends in the history of life persist despite the occasional random events. One line of evidence in support of this view is the ubiquity of convergence. Consider, for example, studies of Jurassic and Cretaceous fossil mammals that evolved during the “Age of Dinosaurs” and long before the modern, placental mammals. Paleontologists have identified a Jurassic beaver (*Castrocauda*), a fossorial (digging) insectivore (*Fruitafossor*) analogous to an armadillo or an aardvark, and even a Jurassic “bat” (*Valticotherium*) [20]. A more recent example is of saber-toothed cats, more generically known as hypercarnivores because of their extreme specialization. Americans are familiar with saber-tooth cats from the La Brea tar pits in Los Angeles, but such cats evolved at least five separate times during the Plio-Pleistocene (the past few million years) as a result of the abundance of large prey species. And one of the five species was not a true cat at all, but a marsupial, only distantly related to true cats. A final example comes from work on the radiation of a single group of spiders in Hawaii [14] and lizards in the Caribbean [19]. Both the spiders and lizards have diversified into different color morphs on different islands. For the Hawaiian spiders, it is possible that all of the green spiders, for example, could have been descendents of a single green spider that dispersed to different islands from the island where it first arose. But when researchers developed a highly resolved phylogeny (evolutionary tree) they found that in each case independent radiations occurred on each island, so that the various green spider species were only distantly related to each other. In other words, the same color morphs appeared independently on different islands. Caribbean lizards displayed a similar pattern. In each case, evolution generated a very similar morphology because of the similarities in ecological opportunities and evolutionary responses. Similar spiders appeared on different islands because similarities in the structure of the environment and the ecological communities produced an ecological opportunity (or niche) on a variety of different islands within the Hawaiian archipelago.

The ubiquity of convergence and parallelism in evolution, even, in the case of Jurassic and modern beavers separated by some 170 million years, demonstrates several points about evolution: (1) There is a structure to

ecosystems that produces similar opportunities in similar environments; (2) sufficient evolutionary variation is available within some lineages to take advantage of these opportunities essentially (to a geologist!) simultaneously; and (3) over longer durations, these opportunities can persist, or at least recur over tens of millions of years. This line of reasoning suggests that while contingent events may interrupt long-term trends, and even remove once-favored groups, enough structure remains so that the patterns will become re-established (see also Vermeij [41]).

The history of life is unlikely to be explicable either as a product of pure contingency, or as purely a result of pervasive trends, but as a more complicated mélange of the two. The challenge for those seeking general laws is, I think, two-fold: First to determine those particular aspects of the history of life where generalities are likely to hold; and secondly, to establish the boundaries of such generalities. Many generalities may be universal through the history of life, as appears to be the case with certain scaling relationships. Others may apply only over a limited range of clades or environments, or for specific intervals of time, until the rules change through biotic crisis or some other cause.

This dichotomy misses a deeper issue, one that reflects the anomalous role of history in evolutionary thought. In *The Origin of Species* Charles Darwin articulated the concepts of evolution, descent with modification, and natural selection (adding sexual selection in a latter book). Since the 1940s the leading intellectual perspective on evolution (known as the Modern Synthesis or the Evolutionary Synthesis) has been framed around the field of population genetics. Population genetics has developed an enormously powerful set of mathematical and analytical tools for understanding the role of changes in the frequencies of genes over time through selection, drift and mutation. This work has established evolutionary biology as a far more robust discipline than was the case earlier, but the Modern Synthesis is a curiously ahistorical view of a historical discipline. Beyond the fact that it provides little insight into how form evolves (something we know now a great deal about from comparative studies of molecular developmental biology), the Modern Synthesis is silent (and indeed probably antagonistic) to issues such as whether the nature of variation upon which selection can act has systematically changed over time, whether the relative significance of selection, mutation and genetic drift (the principle drivers of evolution) has changed over time, or how the changing structure of ecological relationships has altered evolutionary opportunities through time.

The changes in historical processes are more obvious: the economic foundation of societies has changed from hunter-gatherers to agriculturalists, with the development of states, through a variety of economic systems over the past millennium: feudalism, mercantilism to various flavors of capitalism. Political systems have undergone similar transformations during this interval,

particularly with the rise of the nation-state. There may be “laws” of history that transcend these changes, and there is little doubt that contingent factors have played a significant role in historical events. But there is a clear pattern of change in the rules by which societies are organized. Here, I think is an area where historical sciences have a great deal to learn from history, and conversely, where the conversation between history and the historical sciences may be most fruitful. The success of any dialog between these two disparate areas must begin with the rigorous establishment of the patterns for which we are seeking to understand the underlying process (as discussed in the early part of this contribution). I think the next pressing question is to understand the different classes of historical processes likely to be primarily influenced by contingency, by pervasive laws, or by rules which themselves evolve over time.

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