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SPECIAL ISSUE

Quo Vadis, Paleontology?

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Studies of the history of life provide an interesting case study of how the questions scientists can ask, and from which they expect reliable answers, change over time. Some of these changes reflect the introduction of new technology or methodological advances in other fields that open new opportunities; other changes reflect an evolving perspective on what constitutes important research questions or the integration of multiple streams of information. In this contribution, I consider the changing nature of questions in paleontology, largely focusing on English-speaking paleontologists since the mid-twentieth century. Rather than bemoaning the field's limitations, paleontologists have pioneered techniques to identify and often correct preservation and collecting biases in the fossil record. Rigorous methods to infer and test phylogenies have been integrated with molecular clock studies to infer branch-points in phylogeny, and with insights from comparative developmental studies, which together inform our understanding of evolutionary dynamics, particularly novelty. Together, these advances have changed the questions paleontologists can address about the history of life, eliminating some questions (particularly in paleoecology), but greatly expanding research programs in other areas as well as collaborations with biologists and other Earth scientists. I suggest that the questions driving paleontologists have evolved from primarily descriptive and explanatory to increasingly analytical and integrative. These trends are briefly illustrated with examples from studies of the Ediacaran-Cambrian diversification of animals, and from studies of mass extinctions.

Keywords

paleontology • fossil record • Cambrian Radiation • mass extinction

1 Introduction

Study of the fossil record matured into the discipline of paleontology in the mid-nineteenth century, a domain charged with describing and documenting the history of life as recorded by fossils, and employing fossils for local, regional, and intercontinental correlation of rocks to refine stratigraphy and the geological timescale, and as tools for the study of the ecology and evolution of past life. The nature and range of the field has changed greatly over time, particularly in its integration with other geological and biological disciplines.

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Here, I examine the changing nature of questions asked by invertebrate paleontologists and paleobiologists, with particular focus on work since the 1950s. The questions asked by paleontologists and their research practices can be broadly divided into four differing epistemological approaches to the fossil record and the history of life: descriptive, explanatory, analytical and integrative. These differing agendas are not sequential, but overlap, so describing them as distinct phases would be inappropriate. But with increasing appreciation for the nature of the fossil record and greater integration with both biology and geology there has been a reorientation of effort, as paleontology has changed from a discipline primarily focused on fossils as specimens to one that employs fossils as one among several avenues for understanding the history of life. Each section begins with a characterization of the research approach before describing how it has been applied to mass extinctions and the Cambrian events. Comparison of the approaches follows in the discussion. Today, many paleontologists may integrate different components depending on their research projects, or the stage of their careers.

Stephen Jay Gould's (1977a) essay on 'eternal metaphors' in paleontological research identified three questions: Is there directionality to the history of life? What is the motor of evolutionary change, and, particularly, what is the relationship between changes in life and the external environment (with Gould recognizing both environmentalist and internalist – although not vitalist – advocates)? And finally, what is the tempo of evolutionary change? Is it gradual or punctuational? In the almost five decades since Gould penned his essay, these issues have attracted sustained attention and considerable controversy. But, in proposing these questions, Gould acknowledged his focus on the evolutionary components of paleontological research, and noted that these questions did not encompass all work in the discipline. Indeed, many paleontologists spend their careers without serious engagement with any of these questions.

My argument here differs from Gould's in that I am concerned with changes in the practice of paleontology and the nature of questions it has asked. My primary goal is not to provide a brief history of paleontology, but rather to consider how we arrived at the current suite of research foci (for studies of the history of paleontology, see Currie 2019; Dresow 2021; Dresow and Love forthcoming; Rieppel 2019; Sepkoski 2005; Sepkoski 2012; Sepkoski & Ruse 2009; and for the earlier phases Rudwick 2008).

The perspective offered here is that of a late career paleontologist rather than a historian or philosopher, and reflects my understanding of the changes in the field, particularly of the interval since the 1950s. The focus here is on invertebrate paleontology and paleobiology in the United States and United Kingdom since the 1950s, as this encompasses most academic participants in the field over the twentieth century and because modern paleobiology grew out of a transformation of invertebrate paleontology (for a perspective from early career researchers, see Dillon et al. 2023). There are several reasons for this focus, including my background, but also because much of modern paleobiology (rather than paleontology) spread from the US and the UK. Other countries certainly have long and vibrant research traditions, but, for historical reasons, these regions contributed less to this transition. There has been a strong tradition of paleontology in Germany since the nineteenth century, but progress in the mid-twentieth century suffered from two factors: the allegiance during World War II of some prominent paleontologists to the Nazis, and, after the war, the fact that the most prominent paleontologist was Schindewolf, who advocated his own evolutionary theory of "typostrophism." As Reif remarked in his analysis of the German response to macroevolutionary theory, the impact of Schindewolf was to retard studies of macroevolution within Germany until the 1980s (Reif 1986). These developments have been detailed elsewhere (Laubichler and Niklas 2009; Rieppel 2013; Tamborini 2017).

This survey differs from others in this special issue. Currie (2024) emphasizes the special epistemic role of specific fossils, but complete or largely complete vertebrate specimens are often so costly and time-consuming to prepare that they have far greater epistemic value than single invertebrate specimens (with a few exceptions such as fossils in amber, the mid-Cambrian Burgess Shale, and equivalents). Watkins (2024) describes the pathways from fossil to data, identifying issues that were obscure to earlier generations of paleontologists, while Wylie (2024) considers the varying temporality of workers who transform fossils into data.

2 Background

The first four sections (to page 152 in the English translation) of Karl von Zittel's (1901) *History of Geology and Palaeontology* provide a historical synopsis, while the remaining six chapters consider different aspects of geology, from the origin of the Earth through stratigraphy. Although much of the book is descriptive, some chapters consider questions such as the origin of rocks and continents. The sixty-one pages of chapter 5 on Palaeontology are a march through fossil groups from plants and invertebrates to mammals. Zittel acknowledges the separation between stratigraphic and biologic paleontology at the opening, albeit with:

> Biologists had, theoretically at least, the more genuine interest in fossil organisms as individual forms of life; for the biologist…the supreme value of palaeontology was the evidence it might bring towards the solution of problems of the genesis and evolution of living forms, determination of species…and many other fascinating subjects for scientific thought and investigation. (Zittel 1901, 363–64)

The next paragraph begins: "The stratigraphical aspect of palaeontology is the chief care of the geologist" (Zittel 1901, 364). Eleven pages later, after describing the contributions of many late nineteenth-century paleontologists, Zittel makes clear his view that few paleontologists are engaged in analytical or integrative studies, with most engaged in descriptive taxonomy or stratigraphic work (see Zittel 1901, 375). Almost 50 years later, in his Presidential Address to the Paleontological Society, J. Brooks Knight, my predecessor as specialist on Paleozoic gastropods at the National Museum of Natural History, voiced much the same concerns as Zittel (and even cited part of one of the quotes above; Knight 1947).

Yet Knight's complaints about the low state of invertebrate paleontology are curious, as other evidence suggests that significant changes in the field had already begun. Although George Gaylord Simpson was a vertebrate paleontologist, his 1944 book had a major effect (Simpson 1944), while Norman Newell (Newell et al. 1953) and Preston Cloud (1948) in the US and Otto Schindewolf in Germany were at the forefront of paleontologists who viewed the fossil record as reliably preserving a greater range of ecological and evolutionary information and thus permitting a wider range of research questions. Simpson's (1944) contribution to the modern synthesis made a compelling argument for the importance of the fossil record in documenting macroevolutionary processes, while in Germany Schindewolf ([1950] 1994) articulated his more unique evolutionary perspective. The possibilities of greater insights into evolution through a synthesis between paleontology and genetics seemed sufficiently promising that, in 1943, the National Research Council of the National Academies established a committee on *Common Problems of Genetics, Paleontology and Systematics* which convened a meeting in 1946 at Princeton University on *Genetics, Paleontology, and Evolution* with 72 international participants (Jepsen et al. 1949). (The only variation in the sea of white men in the conference photo is between light gray suits and dark suits; a few have hats.) In the second volume of the journal *Evolution*, Cloud evaluated claims for 'explosive' evolution, including the Cambrian radiation (Cloud 1948), while a Geological Society of America symposium was held that year on the same topic (Henbest et al. 1952).

But these efforts towards expanding the research scope of paleontology seem to have had limited impact. This is evident from a collection of short surveys of the status of paleontology assembled by R. C. Moore from 61 contributors and published in the *Journal of Paleontology* in 1968. In his introduction, Moore suggests that such 'periodic stocktaking" might "decades hence…have some value as a record of the general status of paleontology near the three-fourths mark in the 20th century" (Moore 1968, 1327). The notes range over topical issues such as biometrics and paleoecology, reports on the discipline from the US as well as Canada, Britain, western Europe, the Soviet Union and eastern Asia (Japan, China and Korea) and a series of reports on clades from diatoms to mammals. Most of the notes cover descriptive and analytical work, with some, like Simpson's on fossil mammals, describing new analytical and statistical approaches. Newell discussed bivalves and Schindewolf ammonoid cephalopods. Newell, writing with Erle Kauffman, is among the most explicit about the importance of studying populations and of evolutionary studies (and uses the term 'paleobiology'), while Schindewolf is forthright about the importance of moving beyond purely descriptive work (although his focus is nonetheless specimen-based). Few of the broader perspectives of the late 1940s and 1950s are evident. Since Moore was never the most intellectually adventurous of paleontologists, it is possible that the coverage reflected his instructions, but, nonetheless, the contrast with papers from the 1940s is evident.

Essential to the epistemological expansion of paleontology were studies of taphonomy (fossil preservation). As Watkins (2024) describes in this issue, fossils used by paleontologists travel a complex path from death to data, a path which informs the sorts of questions for which fossils are useful data. The field of taphonomy explores processes of preservation and began in Germany during the early twentieth century with studies by Abel, Wasmund, Weigelt, Richter and others, culminating in work by Russian paleontologist I. A. Efremov in the 1940s in which he sought to identify generalities in vertebrate and plant taphonomy (see discussion in Olson 1980). Although this work was known to vertebrate paleontologists like Simpson, it had relatively little impact until later, as more paleontologists came to appreciate the importance of taphonomy in controlling what information could be recovered. In a volume marking the centenary of the publication of *The Origin of Species,* Newell provided an insightful analysis of how understanding of the fossil record had changed since Lyell and Darwin, noting the importance of biases and gaps and their influence on the inference of evolutionary processes (Newell 1959). A significant feature of the paper is Newell's assessment of the adequacy and reliability of fossils for addressing evolutionary, phylogenetic, and paleoecologic questions. From the 1980s onward in the United States, Behrensmeyer, Kidwell and Gastaldo played critical roles in establishing taphonomy as a major research focus for vertebrates, invertebrates, and plants, respectively (Behrensmeyer and Kidwell 1985; Behrensmeyer et al. 2000; Kidwell and Behrensmeyer 1988). Although now largely forgotten, paleoecologic studies in the 1970s assumed preservation of information on ecological timescales in deep time, a degree of over-confidence that was corrected in the early 1980s. By the 1990s, paleontologists acknowledged that the fossil record preserves a variety of types of information, with the extent of bias varying with the questions being asked. Today, an assessment of the reliability of datasets is viewed as essential, allowing paleontologists to reliably address a range of macroecological, phylogenetic and evolutionary questions. While philosophers of paleontology have yet to explore this area, taphonomic studies were critical to the growth of analytical and integrative approaches more generally.

New research avenues were also dependent upon a global effort to define the boundaries of chronostratigraphic units and to refine the geological time scale, efforts that are ongoing. Although such work often receives little attention, chronostratigraphy and geochronology are essential to generating a temporal framework for any studies of deep time (Bokulich 2020a; 2020b; Erwin 2006), including globally synoptic fossil databases, which have in turn allowed paleontologists to ask new questions about the history of life.

3 Alternative Approaches to the Study of Life

Here, I consider descriptive, analytical, quantitative, and integrative approaches to understanding the history of life and illustrate each with examples from two research problems: the appearance of animals in the fossil record during the Ediacaran-Cambrian radiation (570–520 Ma), and the major Phanerozoic mass extinctions.

Although the apparent sudden appearance of animal fossils in the Cambrian concerned Charles Darwin in the 1850s and Charles Walcott in the early 1900s, intercontinental correlations of Cambrian rocks remained challenging into the 1950s and 1960s. The basic temporal framework of the biotic events was only established in the mid-1990s through high-resolution uranium/ lead (U/Pb) radiometric dating, and significant uncertainties in inter-continental correlation are still being resolved, with new geochemical proxies being used to interrogate changing environmental conditions. This influences reconstruction of the tempo of evolution. While the soft-bodied fossils of the Burgess Shale provided great insights into the breadth of the Cambrian Radiation after their discovery in 1909, since the 1980s, many similar Cambrian-age deposits have been identified, mostly in China. Phylogenetic studies of these fossils, combined with new molecular-based animal phylogenies, have greatly clarified relationships between animal clades and the tempo of the earliest animal divergences. While descriptive studies of early animals continue apace, such papers are more frequently placed in a broader evolutionary context. Overall, paleontologists and their colleagues in allied disciplines increasingly focus on understanding the inter-relationships among ecological opportunity, genomic and developmental novelties, and changes in the physical environment.

Turning to mass extinctions, in the early nineteenth century, George Cuvier first recognized biodiversity crises from the fossil record of the Paris Basin, and by the 1840s, English paleontologist John Phillips recognized profound outages at the end of the Permian and the Cretaceous, the basis for his division of the Phanerozoic Eon into the Palaeozoic, Mesozoic, and Cainozoic (in English usage) eras based on early views of diversity patterns (Phillips 1860). As global correlation studies increased in temporal accuracy in the 1950s, they spurred renewed interest in mass extinctions by Schindewolf (1963) and in response by Newell (1967). Such interest exploded after the identification of excess iridium from Cretaceous-Tertiary boundary sections was explained as a consequence of the impact of an extra-terrestrial object (Alvarez et al. 1980), and with reports of a periodic extinction pattern over the past 250 million years (Raup and Sepkoski 1984; Raup and Sepkoski 1986). Over the past four decades, work on the major mass extinctions and other biotic crises has been a significant component of paleontological research.

3.1 Descriptive

The empirical foundations of paleontology characterize phenomena: what fossils are present (taxonomy and systematics), to what clades they belong (phylogeny), where and in what environment are they found in time and space (inferred from both morphology and the sediments in which fossils are deposited), and the relationships between units and regions (biostratigraphy, biogeography, and stratigraphic correlation). Descriptive paleontology remains an essential and vital component of the discipline, as it must, with continuing work in essentially every country with a paleontological community.

But over time, the nature of descriptive paleontology has changed, with the most significant change in the past half century being the revolution in phylogenetic systematics, in which simple parsimony methods have given way to increasingly sophisticated Baysian techniques. The rigor of phylogenetic methods was not immediately evident to many paleontologists. In an edited volume on the topic, paleontologist Art Boucot memorably wrote: "After stripping away the jargon … 'phylogenetic systematics' or 'cladistics', call it what you will, is nothing more or less than old-fashioned systematics so plastered over with jargon as to be unrecognizable to the casual reader" (1979, 199). While a good line, Boucot could not have been more wrong. The rigor enforced by tree-thinking reinvigorated systematic practice and, in turn, new insights in fields from biogeography to development. Many paleontological journals now expect a phylogenetic treatment of the clade of interest. For example, *Journal of Systematic Paleontology,* begun in 2003, notes its aims include the publication of manuscripts that "provide novel and impactful results in phylogenetics and systematics and that use these results in ways that significantly advance rigorous analyses of palaeogeography, palaeobiology, functional morphology, palaeoecology or biostratigraphy." Although perhaps less 'glamorous' than explanatory, analytical, or integrative approaches, this is foundational work to much of what follows (Dresow 2021). Moreover, those seeking scientific immortality are better advised to write systematic treatments than publications in *Nature* or *Science* – they have a far longer impact and utility.

The descriptive output associated with the Ediacaran-Cambrian Radiation has been vast, from further describing of body and trace fossils, puzzling out the many problematic forms whose phylogenetic affinities may be unclear, and refining biostratigraphy, to arguing over the placement of key boundaries in the Geologic Time Scale, such as the base of the Cambrian Period and System. The existence of a broader problem agenda associated with the Ediacaran-Cambrian radiation has fueled descriptive paleontology, with the nature of these papers evolving over time. Similarly, while our recognition of mass extinctions and other biotic crises depends upon descriptive work, that has rarely been the primary rationale for the research. Descriptive work on mass extinction established the primary documentary biotic record before and after such events. In the case of the end-Permian mass extinction (EPME) such work in China greatly sharpened our estimates of the pace of both the extinction and the subsequent recovery (Erwin 2014; Shen et al. 2011; 2018). As noted in the section on analytical paleontology, investigations of mass extinctions required the development of a stratigraphic framework to support global correlations, which only began in the late 1950s before coming to fruition starting in the 1970s.

My claim is that at least into the 1940s, and really until the 1970s, most paleontologists had a limited view of the epistemological possibilities of their discipline. Questions about evolution were raised by paleontologists in the late nineteenth and early twentieth centuries, but the fossil record was generally not seen as having an ontologically unique status. Paleontology was seen as supporting mechanisms and processes established by biologists, and then applied, for better or worse, to the fossil record. A crucial aspect of the "paleobiological revolution" (Sepkoski 2012) was the claim that macroevolutionary processes were decoupled from those of microevolution, and thus the proper domain of the paleobiologist. In contrast, the paleoecology of the 1960s and 1970s failed, in part, because it transferred ideas from ecology with little insight. It was largely abandoned in the early 1980s, with publication of key papers on resolution in the stratigraphic record (Sadler 1981; Schindel 1980), before being resurrected with a new problem agenda (Dresow 2023).

3.2 Explanatory

Descriptive paleontology deals with what fossils have been preserved and collected. The adequacy of the fossil record is largely irrelevant for alpha-level, systematic paleontology. Concerns about the adequacy of the record became relevant only as paleontologists began seeking explanations for the patterns observed in the fossil record. In a very broad sense, before the onset of the paleobiological revolution described in the next section, two distinct explanatory traditions were present. The first reflected the widespread view, captured by Charles Lyell and Charles Darwin, that the fossil record was compromised by limited preservation. This view persisted into the mid-twentieth century in textbooks such as Moore, Lalicker, and Fischer's (1952) *Invertebrate Fossils*, which was still widely used into the 1980s. A second tradition first appeared with early nineteenth-century German Romanticism, and incorporated some late nineteenth-century views of evolution in which the fossil record was read as a relatively unbiased history of life. This view provided support for sudden transformation, non-Darwinian evolutionary theories, and for the directed, progressivist orthogenic views of some German paleontologists and the American vertebrate paleontologist Henry Fairfield Osborn in the early twentieth century. Two features distinguish the early explanatory approaches from later work: a failure to directly examine the strength of the record (before Derek Ager's [1972] revolutionary book *The Nature of the Stratigraphical Record*), and reliance upon explanatory frameworks imported from adjacent disciplines, particularly ecology, evolutionary biology, phylogeny, and functional morphology.

As noted earlier, the development of taphonomy in Germany from the 1920s, and much later developments in the US, challenged both traditions. Each tradition made assumptions (albeit diametrically opposed ones) about the adequacy of the record, rather than treating the record's adequacy as a topic for investigation. Once those assumptions were challenged, explanations for fossils patterns more reliably addressed evolutionary, ecological, biogeographic, and taphonomic problems. For example, beginning in the late 1940s, Newell began investigating the middle Permian Reef Complex of West Texas (primarily in the Guadalupe Mountains). While some of the graduate students engaged in descriptive studies of the silicified invertebrate fossils, the overall goal was to study the paleoecological development of the reef complex. The work of Newell and his team was deeply informed by their winter studies of modern reefs off Bermuda (Newell 1957; Newell et al. 1953). As revolutionary as Newell's study was for its time, subsequent work would show that the uniformitarian assumptions underlying it were flawed, with the reef complex structured very differently than modern reefs (Wood et al. 1994).

Many of the principal questions about the Cambrian explosion involved the quality and reliability of the fossil record. In *The Origin of Species*, Darwin discounted the apparent abruptness of the appearance of fossils at the base of the Cambrian as an artifact of poor preservation of fossils in earlier rocks. Charles Walcott endorsed this view in the late nineteenth and early twentieth centuries with his 'Lipalian Interval' (Yochelson 2006). Others disputed this view, leading to a long-lasting controversy over whether the 'explosion' was real or an artifact of poor preservation (essentially a controversy over rate). But inadequate global correlations and geochronology limited the explanatory power of these discussions; they simply could not be resolved. A further point of controversy came over the nature of 'higher taxa' (phyla, classes, and orders in Linnean systematics), a prelude to later controversies over whether distinct mechanisms drove macroevolutionary processes.

One can identify an explanatory phase of work on mass extinctions from the 1940s into the 1980s, particularly after Newell's 1967 paper. Examples include studies associating the end-Permian mass extinction with the formation of the supercontinent of Pangaea, reflecting the early excitement over plate tectonics (Valentine and Moores 1973). I characterize such research as explanatory because much of this work proposed narrative explanations for events identified in the fossil record, and while such narratives were often plausible, explicit hypothesis testing was infrequent.

3.3 Analytical

The "paleobiological revolution" of the 1970s and 1980s reflects a fundamental shift in the nature of research, as a younger cohort of paleontologists exploited earlier efforts from the 1940s and 1950s, and particularly suggestions from Simpson and Newell, for the discipline to define its own research agenda (Sepkoski 2012; Sepkoski and Ruse 2009). They forcefully rejected claims that the fossil record was inadequate to the task of revealing insights into macroevolutionary dynamics, and began to develop increasingly rigorous methods to test competing explanations. This goal was clearly articulated by proponents of this shift, including David Raup, Stephen Jay Gould, Jim Valentine, and Tom Schopf. This declaration of independence would be contentious well into the 1990s among other paleontologists and within the broader evolutionary biology community. The punctuated equilibrium of Gould and Niles Eldredge, species selection and sorting as articulated by Steve Stanley and David Jablonski, and a greater emphasis on quantifying rates and patterns of taxonomic, morphologic, and ecologic diversity were central to this approach. Although Eldredge and Gould's punctuated equilibrium debuted as an effort to extend evolutionary biologist Ernst Mayr's theory of speciation by peripheral isolates into the fossil record, by the late 1970s, it was enveloped by a broader effort to assert dynamically unique macroevolutionary processes decoupled from adaptation and natural selection at the species level and below.

The analytical turn in paleobiology was dominated by studies of diversity patterns. Harland (1967) published the first modern compilation of fossils, which led to an early description of Phanerozoic marine diversity patterns (Flessa and Imbrie 1973). Sepkoski's compendium of the first and last occurrences of marine fossil families and genera facilitated the treatment of species as "particles in time and space," as Raup once put it. Sepkoski initially released a database of marine families (1982; 1992), followed by his generic compendium (2002). The success of studies building off this work motivated compilations of insects (Labandeira and Sepkoski 1993), terrestrial plants (Niklas et al. 1985) and vertebrates. Such databases with global coverage would not have been possible until the international effort to develop global biostratigraphic correlations began the late 1950s and 1960s. The replacement of 'passage beds' (as in: "late Silurian beds passed upwards into the Lower Devonian") with internationally recognized Global Stratotype and Points (GSSP) defining the base of units of the timescale was essential to improved correlation (Bokulich 2020b). Finally adopted in 1977, the contribution of the GSSP architecture to the paleobiological revolution has often been missed.

As Sepksoki realized, a variety of artifacts plagued a naïve reading of raw diversity data, so considerable effort was expended on developing statistical techniques to analyze and correct the data. Description of an apparently periodic pattern in his marine data (Raup and Sepkoski 1986; 1988) provided further support for the view that the fossil record offered unique information on the history of life inaccessible to evolutionary biologists working with living species. But mass extinctions were seen as a further level of decoupling of macroevolution from microevolution (Jablonski 1986; 2005). Concerns over reliance on the first and last occurrences eventually contributed to the construction of a variety of specialized databases, as well as much larger compilations such as the Paleobiology Database (which emphasized specific localities; Alroy et al. 2008) and the Geobiodiversity Database (which focuses on stratigraphic sections to document the Chinese marine fossil record; Fan et al. 2020). The core of analytical paleontology had two primary goals: to confirm the independent status of macroevolution within the broader field of evolutionary biology and to implement a more quantitative approach to understanding the fossil record. Although macroevolutionary studies remain controversial among some evolutionary biologists, they have become well-established among younger generations of paleontologists and evolutionary biologists.

Although the paleobiological revolution also emphasized quantitative studies, this new work was accompanied by a resurgence of interest in taphonomy and preservation. Questions such as how fossils become preserved and what types of information can be recovered from them became important (as discussed in this issue by Watkins [2024]). If the central claim of the paleobiological revolution was that the fossil record was more reliable than had been assumed since the mid-nineteenth century, this claim had to be supported by empirical studies. As Dresow has recently detailed (2023), a revolution in understanding the nature of stratigraphy began in the late 1970s with Ager's book, mentioned earlier, and sequence stratigraphy. These developments fostered stratigraphic paleobiology – a new way to assess how patterns of sedimentation influenced the distribution of fossils in the rock record.

The expansion of analytical paleobiology was met with controversy within the US paleontological community, in Europe, and elsewhere. When the Paleontological Society established the journal *Paleobiology* in 1974 (with the first issues published in 1975), there was sufficient concern surrounding this boondoggle that the journal was made financially independent so that its expected collapse would not bankrupt the Society. *Paleobiology* was a success from the first issue, but the financial wall remained until about 2010. At the 1986 North American Paleontological Convention in Boulder, Colorado, a prominent US Geological Survey paleontologist decried the growth of "casual theorists and taxon counters." By the next morning, many of the younger paleontologists (myself included) had proudly added "CTTC" to their name badges. Subsequent generations have used new journals to declare their independence. *Palaeontologia Electronica* was founded in 1997 by an international consortium as an open-access, peer-reviewed electronic journal, for example, and other ventures followed.

Another transformative development in the 1980s and 1990s was the widespread adoption of phylogenetic methods (cladistics) within paleontology, as noted under the descriptive section. Vertebrate paleontologists were the first to apply phylogenetics to fossils. Today, phylogenetic methods enable many other studies, including analyses of diversity (lineages through time), comparisons of changes in diversity with morphologic disparity, and the analysis of patterns of character change. It is perhaps surprising, therefore, that the incorporation of phylogenetic methods was historically somewhat independent of the analytical move within paleontology.

Changes in morphology are mediated by changes in developmental patterning, and paleontologists have long been intrigued by such processes. In 1977, Gould's *Ontogeny and Phylogeny* described the history of work since Haeckel and von Baer (Gould 1977b). The book coincided with, and promoted, increased interest in heterochrony (documenting changes in evolutionary patterns). While much work from the 1970s into the 1990s documented heterochronic shifts across animals and plants (McKinney 1988; Bonner 1982), there was an underlying limitation, because too little was known about the underlying mechanisms. Valentine and Campbell (1975) applied Britten and Davidson's early model of gene regulatory networks to the deep past in 1975. But it was not until the late 1990s, when tremendously rapid technological advances allowed the discovery of deep homologies in developmental patterning across animals, that a mechanistic understanding began to emerge (Carroll 2001; 2008). Although this crosses over to the integrative approaches discussed in the next section, over the past three decades an extraordinary discussion has emerged between developmental biologists and paleontologists on the evolutionary processes underlying arthropod and vertebrate limbs, the diversification of sea urchins, and the early origin of animals. Many vertebrate paleontologists (but fewer invertebrate paleontologists) have incorporated evo-devo approaches into their research programs.

Somewhat curiously, analytical approaches to the Ediacaran-Cambrian explosion have been less common. The most obvious impact was the adoption of quantitative approaches to morphological diversity (known as disparity) after Gould published *Wonderful Life* (Gould 1989), leading to a debate over Gould's claims for higher disparity during the Cambrian (see Erwin 2007; 2015). Investigations of disparity subsequently became a significant component of analytical work, and have become even more important as they were combined with results of phylogenetic studies to project phylogenetic relationships within an evolutionary space to form phylomorphospaces. More generally, phylogenetic studies have been critical to resolving the affinities of many Cambrian taxa, but, as noted, these were an add-on to the analytical paleobiology toolkit. Fundamentally, the Ediacaran-Cambrian event was an episode of major morphological novelty among large-bodied bilaterian clades with low taxonomic diversification. Hence, much of the armamentarium of analytical paleobiology was not relevant. Moreover, as discussed in the next section, the critical issues involved unraveling the interactions of evolution and the environment and whether the explosion, if real, was due to environmental changes such as increased amounts of oxygen, changes in ecology, or genetic/developmental novelties (Erwin 2021; Erwin and Valentine 2013; Wood et al. 2019).

As described earlier, the Sepkoski and Raup analyses of Sepkoski's dataset identified the five 'great' mass extinctions as anomalies from background extinction rates (end-Ordovician, late Devonian, EPME, end-Triassic and K/T). Studies of extinction periodicity and the evolutionary implications of mass extinctions, including whether mass and background events were effectively decoupled, were significant components of analytical paleontology. Analytical approaches made significant contributions to statistical testing of the rapidity and reliability of the EPME and K/T mass extinctions (Jin et al. 2000; Marshall 1990; 1994), techniques which spread to other events. Ultimately, however, the reliance of many analytical studies on synoptic databases limited their utility for questions requiring high temporal or spatial resolution. These databases, like Sepkoski's and the PBDB, required coarser temporal resolution than was useful for interrogating the causes and consequences of mass extinction. Doing so required extensive fieldwork in collaboration with stratigraphers, geochemists, and other geologists, a feature of integrative approaches to the fossil record, to which we now turn.

3.4 Integrative

There is a vast suite of questions about the history of life in which paleontology or paleobiology provides only one of several toolkits required to make meaningful progress. Even addressing descriptive questions increasingly requires interactions with other disciplines, with biologists providing insight on anatomy, function, and phylogeny, for example, or the absolute ages of rocks from uranium-lead and potassium-argon dating of interbedded volcanic ashes furnished by geochronologists (Bokulich 2020a). The development of high-resolution geochronology and other chronological methods has been essential to generating the refined temporal frameworks necessary to test alternative causal hypotheses. My distinction between analytical and integrative approaches is that, for the latter, the fossil record alone is insufficient to resolve research questions. Other approaches must be integrated with fossil data.

Preston Cloud began his career as a brachiopod systematist in the late 1930s, and moved first into explanatory approaches, before becoming a prominent advocate of both evolutionary and integrative research. Indeed, Cloud was the first American paleontologist to champion the term 'geobiology' as an integrative approach essential to understanding the history of life. Cloud's promotion of integrative approaches reflected his work on Archean and Proterozoic life which had long depended on discriminating fossils from pseudofossils using tools from paleontology, geochemistry, stratigraphy, tectonics, and microbiology.

Some examples of problems requiring integrative studies are those associated with major mass extinctions, the Ediacaran-Cambrian radiation of animals, the Late Paleozoic Ice Age, and Mesozoic anoxic intervals, among others. Others are more abstruse, such as divining the processes involved in the replacement of fossils by silica, which requires paleontology, sedimentology and geochemistry. Ideally, where resources permit, research projects combine specialists in different disciplines for joint fieldwork and coordinated analytical studies. Regrettably, in the US the National Science Foundation has done a poor job of facilitating such projects.

The critical importance of integrative approaches became clear in the response to publication of the impact hypothesis for the Cretaceous/Tertiary (K/T) mass extinction (Alvarez et al. 1980). The controversy placed specialists in sedimentology, stratigraphy, geochemistry, planetary geology, volcanology, impact studies as well as physics, astronomy and other disciplines in conversation, as their insights were at least as essential as paleontology. The first multi-disciplinary conference on the K/T and impacts more broadly was held in October, 1981 in Snowbird, Utah (leading this and subsequent meetings to be described as “the Snowbird conferences”). Of the 50 contributions to the resulting Special Paper of the Geological Society of America, only 17 were authored by paleontologists (Silver and Schultz 1982). This pattern continued through subsequent Snowbird conferences and many publications on the K/T mass event. A recent test of impact versus volcanic scenarios as extinction drivers involved 36 authors synthesizing biotic, climatic and carbon cycle records at high resolution and modeling the effects of each scenario, concluding that the evidence strongly supported the impact scenario (Hull et al. 2020). Contributors to this paper encompassed foraminiferal paleontology, paleoceanography, geochemistry, modeling, impact studies, and the dynamics of large igneous provinces. Only by integrating such diverse approaches could these alternative scenarios be rigorously tested.

A similarly integrative approach has emerged for explorations of the Ediacaran-Cambrian radiation, where over the past few decades, field work involving paleontology, geochemistry, stratigraphy, and high-resolution geochronology has been just as important as phylogenetic analyses combining fossil and extant taxa and insights from comparative evolutionary developmental biology. Indeed, the variety of disciplines contributing to understanding this episode is impressive, but also challenges the ability of any individual to grasp the full range of research. But it has long been clear that the Ediacaran-Cambrian event no longer ‘belongs’ to paleobiology.

Underlying this integrated approach has been the recognition of dependencies among geochemical cycles, physical processes, and life, whether among microbes, early animals, or Neogene grasslands. The strength of this approach has led to numerous graduate programs in geobiology, now a well-established field, with some departments replacing paleontologists with geobiologists. While some researchers blend both the rigor of analytical paleobiology with the integrated approaches described here, the two pathways have become distinct, often with those pursuing integrated questions undertaking broader work in geology (particularly geochemistry) rather than biology. Integrated approaches almost necessarily involve a commitment to fieldwork, while the analytical approach was pioneered by paleontologists whose field experience was often more limited. Perhaps the most important contrast between analytical and integrative approaches is that while the former has been committed to the reform and improvement of paleobiology as a discipline, the latter sees paleontology as merely one among many tools, with more commitment to the expansion of geobiology than to the reform of paleontology.

4 Discussion

In 1980, Gould captured the opening part of some of the dynamic described here, although Gould was, as ever, focused on the evolutionary dimensions of paleontological research (Gould 1980). He diagnosed two key challenges for the field: an over-reliance on inductive approaches rather than explicit hypothesis-testing, modeling and similar analytic approaches, and a too frequent extrapolation of mechanisms from biology (particularly microevolution) into the deep time of the fossil record. He was certainly correct about both. Gould's contrast of ideographic versus nomothetic approaches captured the beginnings of what David Sepkoski later described as the "paleobiological revolution," and what I have grouped here as part of the quantitative tradition. Of "cladistics," while Gould grudgingly accorded it some value, he did not anticipate the transformative power that phylogenetic analysis would have on all evolutionary studies. But I think the greatest lacunae in his essay is underestimating the importance of a turn back to fieldwork to acquire the data necessary for nomothetic studies (e.g., testing periodicity of mass extinctions or the possibility of drivers from flood basalts or impacts), and that much of the success of paleontology in the past 44 years has come not from declaring paleontology independent, but rather through greater integration with biology and geology, depending on the questions of interest.

As fossils have shifted from being the primary object of study to a "particle in time and space," one component of broader integrative studies, there has been a change not simply in the questions that paleontologists do ask, but the questions they *can* ask. I have sketched a view of how the questions addressed by paleontologists over the past century have changed as the discipline has evolved. Although preliminary, I think this sketch identifies opportunities for philosophers to consider how new questions arise within a discipline beyond the introduction of new technology.

Darwin's descriptions of the incompleteness of the fossil record captured a widespread nineteenth-century view that persisted into the 1970s. What I was taught as an undergraduate about the paucity of the fossil record differed little from the views of Darwin and his colleagues. Although studies of taphonomy and preservation began in Germany in the early twentieth century, they did not have substantial impact on paleontological practice in English-speaking countries until the 1980s. Since then, greater attention to the quality of the fossil record and the nature of fossil preservation has forced paleontologists to recognize that some questions were largely irresolvable (such as fine-scale ecological processes in marine deposits older than a few million years), while also establishing that many deposits are an excellent repository of information for larger-scale questions in macroecology, macroevolution and biogeography, among others. Today, we have a far better understanding of the conditions under which we can explore speciation, for example, or that the time-averaging of many fossil deposits provides paleontologists better data on macroecological patterns and processes than neontologists.

Other changes reflect the introduction of new technology, methodological advances that open new opportunities, or evolving views of important questions. The advent of phylogenetic methods, evo-devo, and new geochemical techniques provide new avenues to understand the history of life beyond the traditional paleontological concerns with fossils. The reciprocal interactions between the Earth and Life have become a major research focus internationally. The conceptual and technological scaffolding required to address many of these new questions was unavailable in earlier decades, while the challenging nature of the research questions surrounding events such as the end-Cretaceous mass extinction and the Ediacaran-Cambrian radiation of animals attracted scientists far beyond paleontology, bringing new approaches and sharpening analytical rigor. But integrating diverse information streams is an increasing challenge which has been addressed by the expansion of interdisciplinary research teams. One consequence is that while the study of the history of life is a vibrant and exciting area of research, paleontology as a discipline may be evolving into something new.

This contribution has focused on trends on invertebrate paleontology and paleobiology. Invertebrate paleontologists, like their micropaleontological colleagues, have been primarily trained in geology or earth science departments, with varying degrees of ancillary training in aspects of biology. Over the past two decades, the more broad-minded programs in evolutionary biology have expanded to include macroevolution, particularly as evo-devo and phylogenetics have increasingly addressed it. Micropaleontology has historically had a closer connection to stratigraphic questions (and thus the petroleum industry) and to paleoceanography through the Deep Sea Drilling Program (1968–1985), Ocean Drilling Program (1985–2004), and Integrated Ocean Drilling Program (2004–present). Paleontologists specializing in vertebrates have largely been trained in biology or anatomy departments while paleobotanists have come from a mix of geology and botany programs, but have often been closely allied to their botanical colleagues. The conceptual trends in these fields, particularly for vertebrate paleontology, sometimes depart substantially from those of invertebrate paleontology. Finally, paleontologists specializing on the Quaternary (2.58 Ma–present) are often closely linked to modern ecology and human evolution programs, with different journals, disciplinary meetings, and intellectual agendas. An interesting avenue to explore would be the trajectory of connections and divergences between these subdisciplines. For example, vertebrate paleontology adopted phylogenetic methods more rapidly in the 1980s than did invertebrate paleontology, whereas quantitative diversity studies diffused from paleobiology to other fields.

5 Conclusion

The central research questions in paleontology have evolved and expanded: from a focus on the description of fossils and their stratigraphic relationships, through an increased emphasis on documenting the history of life, and greater integration with allied disciplines, from geochemistry to ecology, evolution, and phylogenetics. This expansion in the scope of questions in the history of life is challenging for young paleontologists. Several decades ago, research students developed expertise in a particular clade and a time interval (e.g., Cretaceous bivalves). In many graduate programs in English-speaking countries, this gave way to first identifying research questions and appropriate methods, before deciding on the most useful group for the study. While most paleontological research still requires a significant investment of time to learn the anatomy, morphology, systematics and evolutionary history of a particular group, acquisition of these skills are accompanied by honing analytic skills, or by the ability to interpret and integrate work in geochemistry, evo-devo, phylogenetics, or other fields. If one is interested in phylogenetics or evo-devo, fossils may primarily serve as a source of new characters and character combinations, and as a means of dating nodes on an evolutionary tree. In a sense, paleontology has become a victim of its success. Whereas the history of life was once primarily the dominion of paleontology, scientists with a broader array of disciplinary backgrounds have now taken an interest. But this risks rendering traditional paleontology almost irrelevant. In my view, the most successful training programs now meet this challenge by expecting students to become historians of life, not just students of fossils. Are their students paleontologists? Many now describe themselves as geobiologists; others are housed in biology departments as macroevolutionists or phylogeneticists. What these students share is the use of fossils or evidence from the fossil record to understand both pattern and process in the history of life. But, in many cases, the primacy of fossil specimens has receded. While the study of fossils in the context of the history of life will continue, it is less clear that paleontology as a discipline will survive the next few decades.

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