

EVOLUTIONARY PALEONTOLOGY AND THE FOSSIL RECORD: A HISTORICAL INTRODUCTION

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Abstract—From the beginning of paleontology's existence as a distinct professional community in the early 20th century, paleontologists have argued about 'where' the discipline fits among the natural sciences. Long told that paleontologists ought to be content with a subsidiary role as mere documenters of evolutionary change or as stratigraphical 'handmaidens' to geology, over the past hundred years many paleontologists have actively resisted restrictive pigeonholing and attempted to establish paleontology as an autonomous discipline with status equal to its cousins biology and geology. This essay will survey some of the efforts at paleontological 'activism' over the past century, focusing particularly on institutional placement, intellectual contributions, and teaching practices. I will argue that, while no single professional 'identity' defines all paleontological activity during this period, over the first hundred years of the Paleontological Society's existence paleontologists have successfully advocated for increased respect, authority, and autonomy within the natural sciences. In particular, paleontological contributions to understanding of ecological relationships, broad patterns of evolutionary change, extinction dynamics, and adaptive morphology have given paleontology a prominent (though often underappreciated) place in the history of modern evolutionary biology.

INTRODUCTION

The health of a scientific discipline is directly related to the quality of its sources of data. Paleontology has a rich source of data in the fossil record, but opinions have differed over the years concerning the completeness of that record and its adequacy for drawing conclusions about evolutionary patterns and trends. More recently, paleontologists have been enthusiastic about the quality of the fossil record, and estimates of its completeness have been optimistic (Valentine et al., 2006; Benton, 2003; Jablonski et al., 2003; Foote and Sepkoski, 1999). During the hundred years or so after the publication of Charles Darwin's *Origin of Species*, however, paleontology's ability to participate fully in discussions about evolutionary theory was severely hampered by perceptions—from both within and outside of paleontology—that the fossil record was not a complete or reliable source of data. As paleontology established its professional identity during the first half of the 20th century, then, a crucial task for

paleontologists was to establish the adequacy of their data and to answer questions concerning the legitimacy of paleontological contributions to evolutionary theory. Part of this program included determining the proper relationship between paleontology and its two most closely allied sibling disciplines, geology and biology. Without this advocacy on behalf of its data, paleontology might never have claimed a place at the 'high table' of evolutionary biology, and the modern discipline of paleobiology might never have existed.

One of the most profound ironies in the reception of Darwin's *Origin of Species* was its effect on the development of the professional discipline of paleontology. In the early 19th century, when the methodology and disciplinary orientation of paleontology was emerging, modern scientific fields as we know them today did not exist. In 1859, the term 'biology' was still a relative recent innovation, and Darwin himself did not use the term in any edition of *Origin of Species*, preferring to call himself a 'naturalist,' and his discipline 'natural history.'¹ The word 'palaeontol-

¹ On the use of the term 'biology' in mid 19th-century scientific literature, see (Whewell, 1847: p. 544).

ogy' was in general use—Charles Lyell defined it in his monumental *Principles of Geology* as “the science which treats of fossil remains, both animal and vegetable”—but it would have been quite unusual for a scientist to identify solely as ‘a paleontologist’ or even ‘a geologist’ (Lyell, 1830: vol. 3, p. 281).² Therefore the professional status of paleontology, particularly in comparison to the field of biology, is a moot question during the period before those disciplines had become widely recognized as autonomous fields.

Nonetheless, paleontological and geological evidence were vitally important to Darwin in establishing his theory of evolution, particularly because the historical evidence of the fossil record enabled him to argue for temporal evolutionary succession. In the first and successive editions of the *Origin*, Darwin spent many pages discussing the significance of fossil succession, and it is no exaggeration to say that paleontology formed a major pillar of his argument for evolution. However, Darwin’s conservative assessment of the completeness of the fossil record seriously hampered the ability of later paleontologists to fully join in the developing community of evolutionary biology. One of his greatest anxieties was that the ‘incompleteness’ of the fossil record would be used to criticize his theory: the apparent ‘gaps’ in fossil succession could be cited as, at the very least, negative evidence for the gradual and insensibly graded evolution he proposed. Darwin’s dilemma, then, was that he simultaneously needed and was embarrassed by the paleontological evidence in the fossil record. While Darwin almost certainly did not intend to diminish paleontology’s status, his diagnosis of the limitations of fossil evidence had exactly that effect for nearly 100 years following the publication of the *Origin*.

This problem is particularly interesting, because it appears to be a case where a rhetorical strategy influenced subsequent empirical investigation. One of Darwin’s signature argumentative techniques in the *Origin* was to anticipate and overcome potential criticisms of his theory before they were posed. Darwin devoted an entire chapter, “On the Imperfection of the Geological Record,” to weaknesses in the fossil record. Even as he made the case that fossil data were vital for a true understanding of organic history, he cit-

ed the absence of transitional forms between species as an inherent and insoluble problem for geologists and paleontologists. For example, while he defended the conclusions he drew from fossil evidence, he also commented “we have no right to expect to find in our geological formations, an infinite number of those fine transitional forms, which on my theory assuredly have connected all the past and present species of the same group into one long and branching chain of life” (Darwin, 1964: 301). Famously, the metaphor Darwin chose in his apology for the fossil evidence was that of a great series of books from which individual pages had been lost and were likely unrecoverable. “I look at the natural geological record” he continued, “as a history of the world imperfectly kept, and written in a changing dialect; of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines” (Darwin, 1964: 310-11). In other words, not only was the fossil record *currently* incomplete, but it would in all likelihood *remain* that way, no matter how much further investigation paleontologists carried out.

As a number of scholars have noted, this metaphor was not Darwin’s own invention (Herbert, 2005: p. 326). He first encountered it while reading Lyell’s *Principles of Geology*, where Lyell likened the geological record to an encyclopedia written in an ancient language of which we are at best able to translate only a small part (Lyell, 1830: vol. 1, p. 461-2.) Darwin recorded his approval of this metaphor in his “Notebook D” of 1838, where he praised “Lyell’s excellent view of geology, of each formation being merely a page torn out of a history, & the geologist being obliged to fill up the gaps, is possibly the same with the philosopher, who has [to] trace the structure of animals & plants—he get[s] merely a few pages” (Darwin, 1987: p. 352-3). The metaphor continued to dominate Darwin’s thinking about the evidence of transmutation in the fossil record: in “Notebook E,” begun in 1839 (but not completed until 1856), he endorsed Adam Sedgwick and Roderick Murchison’s view of gradational organic change and asked whether “we give up the whole system of transm[utation], or believe that time

² By 1859, however, Darwin was referring to predecessors and contemporaries as ‘paleontologists’ and ‘geologists,’ including Georges Cuvier, Richard Owen, Louis Agassiz, Adam Sedgwick, and Lyell. See (Darwin, 1964: p. 310).

has been much greater, & that systems, are only leaves out of whole *volumes*” (Darwin, 1839-56: p. 127, in Barrett et al., 1987: p. 433).³

Since the metaphor of the incomplete book clearly had wide currency in the middle part of the 19th century, the ‘blame’ for its corresponding (and discouraging) message to future paleontologists cannot be laid entirely at Darwin’s door. But it is important to note that in an *evolutionary* context, the incompleteness of the fossil record has much more significance than it otherwise would. While Lyell eventually accepted transmutation, his *Principles* assumed that organic form was static, and his geology adhered to the strict uniformitarian view that the conditions and processes of the earth and its inhabitants did not vary greatly over time. Transitional forms were not expected, and if organisms were missing from particular localities or strata where they were expected to be found, they were likely simply waiting to be discovered in some other place. Sedgwick’s case was even easier: as a follower of Georges Cuvier’s ‘catastrophist’ geology, he actually *expected* gaps to be present in the geologic record, which corresponded to Cuvierian ‘revolutions’ or cataclysmic, transformative events.

It was thus only after transmutation came into the picture that the completeness of the fossil record became a significant issue. Darwin’s theory revolutionized paleontology, since the fossil record became the only potential source of evidence that evolution had occurred and for interpreting the history of organic change. Without evolution, paleontology merely made interesting, descriptive observations about the form and distribution of once-living creatures; without paleontology, there was no concrete evidence that evolution had happened. But on its own, paleontology could offer no independent contribution to evolutionary theory, since that theory depended on evidence from biology, breeding, biogeography, geology, heredity, and other fields in order to make the paleontological data meaningful. In other words, paleontology without the support of evolutionary theory could not decisively settle any questions about the nature of organic history—it *required* Darwinian evolutionary theory to contextualize its contributions, and at the same time to excuse its flaws. Darwin had stated, more or less,

that paleontology had already provided everything it was likely to contribute to understanding evolution, so for supporters of Darwin there was no great urgency to scrutinize the fossil record. In fact, Darwin’s supporters were more likely to want to push paleontology into the background: as historian William Coleman argues, “to the biologist that [fossil] record posed more problems than it resolved.... the incompleteness of the recovered fossil record, in which a relatively full historical record for any major group was still lacking, was the very curse of the transmutationist” (Coleman, 1971: p. 66).

PALEONTOLOGY AFTER DARWIN

Of course, not every paleontologist in Darwin’s day accepted Darwin’s dismal conclusion about the fossil record or its message for the future contributions of paleontology. For example, Darwin’s countryman and contemporary John Phillips—a paleontologist who conducted the first thorough accounting of the accumulated fossil record and interpretation of its results—strongly disagreed with Darwin’s position. Phillips is remembered today primarily as having been the first to describe the three great stages in the history of life: the Paleozoic, Mesozoic, and Cenozoic eras, which corresponded to discontinuities he observed in the proportions of various major taxa present (or not) in the succession of earth’s strata. Phillips depicted the history of life as a series of three overlapping diversity curves, the first two of which terminate as a new curve begins its ascent. Phillips’ model was ambitious for its time, but he defended its legitimacy in part by criticizing Darwin’s opinion that “we possess... merely fragments of the record, which indeed never was complete.” Rather, he countered that “surely this imperfection of the geological record is overrated. With the exceptions of the two great breaks at the close of the Paleozoic and Mesozoic periods, the series of strata is nearly if not quite complete, the series of life almost equally so” (Phillips, 1860: pp. 206-7).

Among Darwin’s close colleagues, the most outspoken apologist for the paleontological record was probably Thomas Henry Huxley. Huxley was recog-

³ Herbert notes that Sedgwick had delivered an address in 1830 where he observed that “a leaf seems to be torn out from the volume of her [nature’s] history.” Sedgwick, 1830, in Herbert, 2005, 326.

nized by his colleagues for his geological and paleontological work by being elected president of the Geological Society of London in 1869, and he spoke and wrote widely on paleontological questions of the day. It is well documented that Huxley differed with Darwin over the origin of new types (e.g. higher taxa), but this did not stop him from defending the Darwinian theory using evidence from paleontology. In his 1870 address to the Geological Society “Paleontology and the Doctrine of Evolution,” Huxley presented a fairly orthodox account of the documentation for evolution preserved in the fossil record, asserting “it is generally, if not universally, agreed that the succession of life has been the result of a slow and gradual replacement of species by species; and that all appearances of abruptness of change are due to breaks in the series of deposits, or other changes in physical conditions” (Huxley, 1894: p. 343).

However, in private Huxley remained unconvinced that the evolution of higher taxa did not involve some form of saltation, or evolution by jumps. To Lyell he famously wrote “The fixity and definite limitation of species, genera, and larger groups appear to me to be perfectly consistent with the theory of transmutation. In other words, I think transmutation may take place without transition.” This did not mean that he rejected natural selection, or even that he doubted gradualism, but at least in the year *Origin* was published he felt the paleontological evidence “lead[s] me to believe more and more in the absence of any real transitions between natural groups, great and small.” Interestingly, though, Huxley did not see his saltationist hypothesis as any challenge to uniformitarianism, and he apparently felt no common cause with the so-called ‘catastrophists,’ since he urged Lyell that his view “is the logical development of Uniformitarianism, and that its adoption would harmonise the spirit of Paleontology with that of Physical Geology” (Huxley to Lyell, June 25, 1859, quoted in Herbert 2005). Nonetheless, he continued to harbor saltatory suspicions throughout his life, and his hesitation (of all people’s) to fully embrace natural selection as the all-powerful agent of evolutionary change testifies to the difficulty 19th century paleontologists had squaring the fossil record with Darwinism.

If Darwin’s reading of the fossil record had difficulty gaining traction even among his staunchest allies, it is easy to understand why many paleontologists less ideologically committed to Darwinism felt compelled

to pursue an entirely different theoretical approach. There is some truth to the perception that paleontology offered few contributions to evolutionary theory between the publication of *Origin* and the period of the modern synthesis, but this interpretation hardly tells the whole story. Many paleontologists did in fact pursue descriptive work in morphology and stratigraphy with very little interest in evolutionary theory, but there was a sizable minority who had genuine theoretical ambitions for their work. This group included a number of prominent late 19th and early 20th century paleontologists, including the American vertebrate specialists O.C. Marsh, E.D. Cope, Alpheus Hyatt, H.F. Osborn, W.D. Matthew, and William Gregory, and on the European side George Mivart, Alexandr Kovalevskii, Othenio Abel, Louis Dollo, Wilhelm Waagen, Karl Alfred von Zittel, and Otto Schindewolf. There were, in fact, a great many paleontologists between 1860 and 1940 who pursued evolutionary theory. The problem was—at least from the perspective of the eventual framers of the Modern Evolutionary Synthesis—these paleontologists pursued the wrong *kind* of evolutionary theory.

It is worth taking a moment to consider what, to a paleontologist, the fossil record seems to indicate about evolutionary processes and patterns, and how that interpretation might differ from the perspective of a biologist. As Peter Bowler points out, 19th century research into systematics was concerned especially with reconstructing fossil phylogenies. This involved arranging fossils into likely sequences based on “structural resemblances” and attempting to extrapolate evolutionary development across morphological and stratigraphic gaps. For this reason, “morphology thus became the first center of evolutionary biology” (Bowler, 1996: p. 41). The problem, however, is that the sequence of morphology in the fossil record does not always clearly indicate the steps in an evolutionary sequence taken by a particular lineage. Fossils are often too rare, too poorly preserved, or just plain missing, and it is left to the paleontologist to ‘connect the dots’ in as likely a fashion as possible. One feature that appears to stand out in the fossil record is the appearance of fairly linear trends, even among distantly or unrelated groups, towards similar morphological features. One manifestation of this tendency is the phenomenon of parallelism, or the tendency for multiple lines of descent to follow “a more or less identical sequence of

morphological stages” after divergence from a common ancestor (Bowler, 1996: p. 70). Another related apparent trend is convergence, where wildly different groups independently settle on the same adaptive response to an environment without the benefit of a recent common ancestor (such as the evolution of wings in birds and bats). The question posed to paleontologists was whether these phenomena can be explained by simple Darwinian natural selection, or whether some other force or mechanism was required.

I will not discuss the basis for these concerns in great detail—interested readers are advised to turn to Bowler’s excellent treatments of the subject—but the short version is that many late 19th century paleontologists were sufficiently impressed by the apparent *linearity* of evolution that they felt compelled to reject Darwinian natural selection as the prime cause (Bowler, 1983: p. 118). ‘Linearity’ should be understood as the appearance of trends in the fossil record that cannot be explained simply as the random product of accumulated adaptive responses to environment—trends (such as increasing body size) that appear to be ‘preprogrammed’ into evolutionary development. The common name for such a belief is orthogenesis, which holds that evolution proceeds in a straight (orthogonal) path along a predetermined trajectory. The essential message of orthogenesis is that trends are produced independently of adaptive fitness, even to the ultimate detriment of a lineage, as in the case of so called senescence or ‘racial senility’ of a group that leads to eventual extinction.

Orthogenesis (and Lamarckism) particularly caught on in America, where Louis Agassiz appears to have played a central role by promoting an “idealist philosophy of nature” from his position as curator of the Museum of Comparative Zoology at Harvard (Bowler, 1983: p. 120). It appealed particularly to paleontologists—and vertebrate paleontologists especially—who were attempting to reconstruct lineages across millions of years based on scant, often incomplete, fossil evidence. E.D. Cope was perhaps foremost in the 19th century American school of orthogenetic paleontology, and his views are preserved in the so-called ‘Cope’s Law’ of accelerating growth. As for the question of why paleontologists, rather than biologists, were drawn to orthogenetic theories, the answer is quite straightforward: trends become apparent only when time is made a dimension of evolutionary study,

and paleontology is the branch of evolutionary biology that deals with the temporal evidence of evolution. Trends have had a persistent interest for paleontologists, and indeed much of 20th century evolutionary paleobiology has been concerned with identifying and evaluating evidence for the appearance of trends in the fossil record. Where 19th century orthogenetic paleontologists ran afoul of Darwinism was in asserting that internal forces guided these trends independently of adaptation; a major task of 20th century paleobiology has been to explain the appearance (and possible genuine existence) of trends without invoking non-Darwinian, speculative mechanisms.

In any case, it is fair to say that by 1900 the promise of paleontology as a central evolutionary discipline, which had appeared so bright in the mid-19th century, had faded considerably. The most spectacular advances in the field had been in the collection of large vertebrate fossils, and broad, empirical studies of evolutionary pattern and process—such as Phillips’ accounting of the fossil record—were not actively pursued. Rightly or wrongly it was also perceived that paleontologists had abandoned Darwinism and natural selection, which alienated those evolutionary biologists who were still committed to Darwinian orthodoxy, and for which paleontology would pay heavily when Darwinism emerged triumphantly in the mid-20th century. Finally, from an institutional perspective, paleontology was in danger of losing all contact with biology: isolated in geology and museum collections departments, paleontologists had little regular interaction with experimental biologists. This led to mutual mistrust and incomprehension between the two fields that was only exacerbated after the ‘genetic turn’ in biology following the rediscovery of Gregor Mendel’s work on heredity. Darwin may have considered paleontology, geology, and biology to be equal partners in the enterprise of evolutionary natural history, but as the 20th century began, they were separated by a fairly wide gulf.

THE PROFESSIONALIZATION OF PALEONTOLOGY AND THE FOSSIL RECORD

It is worth noting that from the beginning of organized, professional paleontology in the U.S., workers had been concerned with addressing the problem of

the adequacy of the fossil record. In 1908, professional paleontology got a lift when the Geological Society of America voted to establish a new society exclusively for paleontologists. When the Paleontological Society (PS) was first established it had just 34 charter members, but that number had quickly ballooned to 96 by its first official meeting in December of 1909 (Schopf, 1980; Dunbar, 1959; Kelley, this volume). In its early years the PS was dominated by invertebrate paleontologists, and this trend continued as demand for invertebrate specialists increased due to their value to the burgeoning oil industry. While the PS was designed mainly to attract academic paleontologists, a parallel society, the American Association of Petroleum Geologists (founded in 1906) and its daughter organization the Society of Economic Paleontologists and Mineralogists (SEPM) represented the interests of geologists and paleontologists in the petroleum industry, and thus initially enjoyed larger membership (Schopf, 1980). When *Journal of Paleontology* (*JP*) was launched in 1927, it was owned not by the PS but rather by SEPM, and its initial mandate was to provide an outlet “primarily for the description of newly discovered microfossils from the oil fields” (Dunbar, 1959: p. 909). Academic paleontologists therefore had practical as well as intellectual reasons to feel somewhat disenfranchised.

The first meeting of the Paleontological Society, held in Boston in 1909, was organized as a “Conference on the Aspects of Paleontology,” and the topics chosen for discussion reflected the broad issues that faced the profession at that time. The first of these topics was the “Adequacy of the Paleontologic Record,” and the two speakers were Samuel Calvin, a professor at the University of Iowa, and Raymond S. Bassler of the U.S. National Museum. Given the general dispute that had been assigned to the fossil record over the years, it may come as a surprise that both men emphasized the relative adequacy of paleontological data. Calvin commented that “The faithfulness with which the paleontological record has been kept since the beginning of the Cambrian is a matter of constant surprise. No organism was too small for preservation, if only its soft parts were supported or protected by a stony skeleton of some kind; no parts of the skeletal

structure were too minute to be kept practically unaltered to the smallest microscopic detail; no period of time has been so long that the records of the large or the small things of life were necessarily obliterated” (Calvin, 1910: p. 582-3).

Bassler’s paper also generally struck an optimistic note, although it did point out some potential limitations of the record, namely that “in quite a portion of the geologic column organic remains are not only poorly preserved, but are, as known at present, very rare.” However, drawing on his expertise as a museum scientist, Bassler enthusiastically described the ways in which “the preparation and study of paleontologic material has progressed to such a point that a poor fossil is no longer a bugbear” (Bassler, 1910: p. 587). These techniques included dissolving obscuring matrix of clay and limestone with “caustic potash” and other chemicals to reveal the underlying fossils, cutting thin sections, and painting fossils with ammonium chloride to highlight fossil structures in photographs. Crude or obvious as these techniques may seem now, such practices also remind us that technology has been an essential component in overcoming limitations of the fossil record, a fact as true in 1910 as any other time. Bassler’s enthusiasm for new techniques was enough to move him to predict not only the reduction of major gaps in the record, but that “it is probably only a matter of time before the complete faunal succession can be established” (Bassler, 1910: p. 589).

Another useful perspective on the development of paleontology over the period leading up through the Synthesis is also provided by a survey of Presidential addresses of the Paleontological Society beginning in the 1910s. The organization’s first president was John M. Clarke, who established the tradition of giving an annual address (in 1910) which continued for much of the 20th century.⁴ While no official mandate determines the subject matter of these addresses, over the years many exiting presidents have taken the opportunity to consider major directions or challenges in the field, and have often explicitly offered a ‘state of the discipline’ assessment.

The first presidential address to strongly advocate the adoption of methods and conclusions from disciplines outside paleontology (such as genetics)

⁴ For a history of the Paleontological Society, see (Schopf, 1980). See also (Rainger, 2001). On early 20th century American paleontology, see (Rainger, 1997); (Rainger, 1993); (Rainger, 1988); (Rainger, 1986); and (Rainger, 1982).

was delivered in 1922 by William Diller Matthew, Henry Fairfield Osborn's long-time assistant in the Department of Vertebrate Paleontology at the American Museum of Natural History. According to Ronald Rainger, Matthew developed a strong personal dislike for Osborn, and Matthew came to reject Osborn's arisotogenetic (orthogenetic) evolutionary theory in favor of fairly orthodox Darwinism. Osborn relied heavily on Matthew's abilities in biostratigraphy and paleobiogeography, and as a result Matthew developed a much greater sensitivity for the accuracy of the fossil record than did his patron (Rainger, 1991: p. 183-4). However, this knowledge led Matthew to downplay the completeness of the fossil record, and encouraged his skepticism about larger, theoretical claims made solely on the basis of paleontological evidence.

Matthew's address to the Paleontological Society, "Recent Progress and Trends in Vertebrate Paleontology," was presented as a critical review of the "adequacy" of the "foundations" (i.e. the fossil data) on which paleontology is built (Matthew, 1923: p. 401-2). Matthew's argument was decidedly ambivalent: on the one hand, he defended the legitimacy of paleontological contributions to evolutionary theory, but on the other, he cautioned paleontologists about overreaching their evidence. Concerning the attitude of many geneticists towards paleontology, Matthew offered that he did "not altogether agree with a distinguished Columbia professor [Thomas Hunt Morgan] who declared not long ago that paleontologists had no business to reason on or draw conclusions from their specimens, but should content themselves with describing and illustrating them." "Nevertheless," he continued, "I do think we should distinguish far more sharply between provisional and tentative conclusions based on scanty and fragmentary data and those which are really proven by adequate evidence" (Matthew, 1923: p. 415). Still, he did hold out hope for paleontology's future contribution to evolutionary theory; ironically this would only be assured by diligent descriptive work documenting specimens in stratigraphic sequences in order to document "the evolution of species and not merely of structures" (Matthew, 1923: p. 417). Then, Matthew argued, "Professor Morgan's strictures on paleontological evolution, which are aimed really at the old methods, not our modern standards, will be no longer justified" (Matthew, 1923: p. 418).

Whether or not as a result of Matthew's influence, the next several presidential addresses to the Paleontological Society—at least the ones that ask broad questions about the field—show an increasing accommodation of the Darwinian attitude towards the fossil record. Joseph Cushman's address on "The Future of Paleontology" in 1937 returned explicitly (and enthusiastically) to Darwin's metaphor of the 'book' in its assessment of paleontology's limitations. He wrote that "to the paleontologist is given a rare privilege, for it is his stewardship of the oldest book of records that we possess, the book which contains all that we know of the progress of life on this planet of ours. True, the book has had very hard usage and is imperfect. Many of its pages are badly torn and blotted; others have later records written across a page of earlier ones, so that it is difficult to trace the written lines. Many of its pages are entirely missing" (Cushman, 1938: p. 359). Cushman did not entirely dismiss the theoretical ambitions of paleontologists, but he did charge paleontologists (as did Matthew) with the mostly descriptive task of filling in links in fossil succession.

Similarly, Lloyd William Stephenson's 1942 "Paleontology—An Appraisal" offered similar language and a similar message. His variation on Darwin's metaphor proclaimed variously that "in Nature's great history book much of the story is recorded," that "the book is in sections, scattered here and there over the face of the earth" with "many pages [that] have not been turned," and that "hints of the contents of the book are gained, but only by turning the pages all the way back is the full story revealed" (Stephenson 1942: p. 376). Interestingly, Stephenson did not comment on 'missing pages' (perhaps suggesting greater optimism than his predecessors) but he did advocate what can only be described as a 'handmaid' role for paleontology among the other sciences: "We must look to the organic chemist, the physiologist, the biologist, and the experimental breeder for discoveries that reveal the actual processes by which the evolution of organisms is accomplished.... it [then] becomes the duty and privilege of paleontologists to seek out confirmatory evidence of evolution offered by fossils" (Stephenson, 1942: p. 377).

The final two addresses we will consider here are both from the mid-to-late 1940s (and therefore presented in the wake of the Modern Synthesis). In considering "Paleontology in the Post-War World," B.F.

Howell described his fellow paleontologists as being “all too prone to look upon themselves as mere hand-maids to geology and to think of paleontology as nothing more than the tail on the geological dog.” He optimistically encouraged his colleagues to rather think of their discipline as “a sister science to biology that both draws from, and contributes to, geology,” and to assert that paleontology “is an independent science, worthy of recognition as such” (Howell, 1945: p. 375). Howell’s positive message was somewhat dampened, however, by his reminder that “since paleontology cannot, because of its nature, be a very exact science paleontologists cannot think or write in such mathematically definite terms as can other scientists as the mathematicians, the physicists, and the chemists, or even as nearly exactly as can the biologists” (Howell, 1945: p. 375). J. Brookes Knight’s provocative title for his 1947 address was “Paleontologist or Geologist,” and his choice of topic was quite similar to Howell’s. Knight, however, made an even more strident argument for the independence of paleontology from geology, and his paper even proposed that universities should establish separate departments for each discipline (Knight, 1947: p. 282). He also argued that paleontology’s subject matter places it more properly among the life sciences than as part of geology, and that invertebrate paleontology in particular should be considered a branch of biology (Knight, 1947: p. 282-3). Knight did not, however, comment on whether paleontology had much to offer biological evolutionary theory; in fact, the impression his address gives is that the benefits from a détente between the two disciplines would accrue mostly for paleontology.

Despite the optimistic note struck by Knight and others, not all paleontologists were ready to drop traditional ties and attachments with geology. Knight’s comments in fact touched off a minor controversy—particularly his statement that “because paleontology is not truly a branch of geology,” he wrote, “it does not best serve geology when cultivated and applied by geologists” (Knight, 1947: p. 282-3). This drew a hostile response from J. Marvin Weller of the Walker Museum at the University of Chicago, who retorted that paleontological stratigraphy is “the heart of geology” and its “single great unifying agency” (Weller, 1947: p. 570; Rainger, 2001). “Invertebrate paleontology is much more closely related to geology than biology”

he reasoned, and the two fields are mutually interdependent, whereas biology and paleontology can each “get along” without the other. He had little time for vertebrate paleontologists, whom he considered hardly even geologists, and even less interest in the kind of paleontological-biological synergy preached by his many of his peers: “any student of fossils who does not have a strong, abiding, and well-founded interest in geology... is not a paleontologist. He is simply a paleobiologist” (Weller, 1947: p. 572).

While Weller’s use of the term ‘paleobiologist’ as an epithet was unusual, his sentiments were connected to quite reasonable concerns about the training and employment of future paleontologists, whom he worried would have inadequate experience with stratigraphy. He worried that the subtraction of geological courses from the standard curriculum would divert student interest from “the really important problems” in paleontology “under the delusion” that paleontological work could answer biological questions (Weller, 1947: p. 574). While he recognized that a paleontologist’s training requires “a good foundation in modern biology,” he urged that this should not come at the expense of geology courses.” More fundamentally, he appears to have been concerned about the potential a) for geology to lose its ability to appeal to bright young students, and b) for paleontology to sacrifice its distinctiveness and relevance among the sciences. Weller noted that “invertebrate paleontology has lagged far behind modern biology in both breadth of vision and accomplishment,” and he warned that “if few geologists are to be interested in invertebrate paleontology this source of recruits would soon dry up and there would be grave danger that invertebrate paleontology would stagnate for lack of active workers” (Weller, 1947: p. 575).

REASSESSING THE FOSSIL RECORD

A turning point for paleontologists would come in the decades immediately following the Second World War, when a combination of new empirical techniques and a new theoretical orientation would lead invertebrate paleontologists to make more definitive claims about the adequacy of the fossil record for evolutionary study. One of the most important of these workers

was Norman D. Newell of the American Museum of Natural History and Columbia University, who perhaps did more to promote the legitimacy of conclusions drawn from analysis of the fossil record than any other paleontologist in the 1950s and 60s. Newell's contributions were diverse and important: he helped pioneer the investigation of broad patterns in the fossil record, the development of quantitative approaches to fossil databases, the study of the evolutionary significance of mass extinctions, and the creation of the sub-discipline of 'paleoecology.' Throughout his career, Newell also tirelessly promoted the institutional agenda of paleobiology, and he trained many of the leaders of the movement's next generations.

In 1948, shortly after arriving at the AMNH, Newell and Edwin Colbert published a response to Weller's critical essay, in which they expressed sympathy with Knight, whom they observed "has done a real service to paleontology and geology in calling attention to serious traditional deficiencies in the training of invertebrate paleontologists" (Newell and Colbert, 1948: p. 264). While Newell and Colbert were aware of the practical obstacles to enacting Knight's vision, they respectfully offered that "Professor Weller's point of view admirably expresses the traditional (and 'narrow') attitude of the geologist toward paleontology," which "is being modified only too gradually." Paleontology is only considered a branch of geology, Newell and Colbert reasoned, "because paleontologists, through lack of adequate training in biology, have made it so" (Newell and Colbert, 1948: p. 265). They proposed a division of paleontology into two categories—stratigraphic and "paleobiology"—and emphasized that even this dichotomy obscured significant areas of overlap between the two approaches. Many of the goals of paleontology transcend stratigraphy, they stressed, such as phylogeny reconstruction and the restoration of the fossil record, but are also beyond the ken of biologists who lack paleontological training. And turning the tables on Weller, Newell and Colbert argued that it is its close traditional association with

geology that has, "as much as anything... [caused] the lack of mature growth of this branch of [invertebrate] paleontology." In their conclusion, Newell and Colbert centered the issue on paleontology's engagement with evolution: "the invertebrate paleontologist in North America has suffered because of his lack of an *evolutionary* viewpoint, the result of a lack of training in biology" (Newell and Colbert, 1948: p. 267).

By the end of the 1950s more and more paleontologists were thinking like Newell, Colbert, and Knight. G. Arthur Cooper's Presidential address in 1958 on "The Science of Paleontology" addressed this problem head-on, and argued for a biologically-oriented paleontology that would nonetheless maintain its independence from its sister field.⁵ Cooper was particularly alarmed by the trend towards exclusively stratigraphic paleontology since the 1920s that saw a concomitant decline in "descriptive, taxonomic, and morphological" work, the latter of which was a "pure or 'old fashioned' Paleontology" to which he wanted the profession to return.⁶ His address offered a list of factors that "conspire to limit the appeal of pure paleontology and even general zoology to the younger generation" (Cooper, 1958: p. 1011). These included the "limited practical and economic value" of paleontology; the difficulty and length of time needed to acquire expertise; inadequate emphasis on 'pure' research (as opposed to fieldwork); "divisive forces within paleontology [which] have tended to destroy its unity"; and inadequate funding. Cooper emphasized, however, that paleontology is "a great field still in the qualitative stage with basic work for several generations," but that effort would be required to recruit students to carry on this task (Cooper, 1958: p. 1014). He proposed a straightforward approach to this problem by changing pedagogy to "emphasize the zoological and biological sides of the subject rather than the stratigraphical," and "reorienting the values" of paleontology accordingly (Cooper, 1958: p. 1015). But although he firmly cast his lot with those who "accept the fact that all life is related and that paleontology is

⁵ Intriguingly, Cooper's address proposed to "revive" the tradition of Presidential speeches, which had apparently been dormant between 1949 and 1957. It is unclear why the practice had fallen off, but after Cooper's address the tradition has continued unbroken up to the present. See (Cooper, 1958: p. 1010).

⁶ It is an interesting (and perhaps unconscious) rhetorical strategy to present non-stratigraphic paleontology as the 'traditional' mode, since others (i.e. Weller and Moore) had done just the same for stratigraphy. Clearly it is desirable to claim one's favored approach as the 'pure' version of a discipline, but historically speaking it is inaccurate to claim that one preceded the other.

in reality paleobiology, an independent science,” his first concern was that paleontologists continue the tradition of morphological description before attacking the larger theoretical problems of evolution (Cooper, 1958: p. 1012). Thus we can see that at this point paleontologists were divided most fundamentally over the biology vs. geology question, rather than over the theoretical import of their subject matter. Nonetheless, Cooper concluded that with sufficient collection of data, while “biology shows the mechanics of evolution... the pattern can only be learned through fossils” (Cooper, 1958: p. 1016).

As even the most ‘progressive’ paleontologists were well aware, however, no interpretation of evolutionary patterns can begin without a reasonable degree of confidence in the fossil record itself. From an empirical standpoint, paleontologists had good reason for increasing confidence in the quality and adequacy of their data. One of the fundamental goals of evolutionary paleobiology was, as Cooper put it, to elucidate the pattern of evolution, and between 1950 and the late 1960s a number of innovative approaches to assessing patterns in the fossil record were developed. A major effort was applied to studying trends in large sample populations, which naturally required a deeper and more thorough understanding of the fossil record. Since invertebrate fossils are far more numerous than vertebrate remains, paleobiology gradually became oriented towards invertebrate paleontology. Vertebrate paleontologists like Osborn and George Gaylord Simpson may have helped inaugurate the paleobiological movement with studies of the evolutionary sequences of fossil mammals, but workers recognized that well-documented evolutionary sequences and reliable representative sample populations were qualitatively less likely to be found in vertebrate lineages. Paleobiology is not, in its essence, an exclusively invertebrate field, but practical and technical limitations and requirements directed the research interests of paleobiologists over the next several decades more and more towards invertebrates.

In 1959, the *Journal of Paleontology* published papers from a special “Symposium on Fifty Years of Paleontology” celebrating the first half century of the PS, and advances in studying the fossil record were highlighted by several papers. Carl O. Dunbar drew attention to improved techniques in the recovery of in-

vertebrate fossils, in particular citing Cooper’s work on the Permian faunas of West Texas. From the standpoint of empirical study of the invertebrate fossil record, Cooper made some of the most significant contributions of the middle 20th century. After completing his PhD at Yale in 1929, he spent a journeyman’s year working for Charles Schuchert on a project to re-survey the entire brachiopod kingdom. Part of his assignment led him to Washington D.C. to examine Charles D. Walcott’s brachiopod collections. This eventually led to a position with the National Museum of Natural History, where Cooper spent his entire career. It was during his early years at the NMNH that he was exposed to the Permian beds in Texas, which he first visited in 1939 with Josiah Bridge. As Cooper later recalled, “the processing of these pieces [collected with Bridge] the next year yielded a harvest of good things but also many fragments suggesting that bigger pieces would yield more complete specimens. Thus was born the idea of etching Permian limestones of the Glass Mountains to produce a complete fauna” (G.A. Cooper to Norman Newell, December 16, 1980. Norman Newell Papers, American Museum of Natural History, Correspondence Box 2). By the early 1950s, Cooper had expanded Bassler’s program of acidic decomposition of limestone to a massive program, joined by colleagues at the AMNH and other institutions. A report from this period gives an insight into how this process yielded such tremendous fossil resources, describing how he had obtained nearly 6.5 million fossils from 60 tons of limestone (G.A. Cooper, Untitled report. Newell Papers, Correspondence Box 2.)

In another paper from the 1959 symposium, Newell gave a more general overview of developments in the appreciation of the fossil record, and explicitly connected those changes to the growth of paleobiology. He began by noting that “from the very beginnings of our science there have been two schools, those who study fossils in order to understand stratigraphy, and those who study fossils in order to learn about past life” (Newell, 1959: p. 489). While he was pleased to report that “the fossil record is much richer than we formerly supposed,” he cautioned that paleontology needed to produce more biologically-sensitive workers to meet the demands of the changing profession. He also cited five “truly revolutionary developments of the past three decades”: 1) improved collection and

preparation of fossils; 2) “recognition of the special importance of populations in taxonomy and evolution”; 3) more attention to ecological context; 4) “the application of statistical methods... [to] all sorts of paleontological problems”; and 5) greater understanding of the geochemistry of fossils (Newell, 1959: p. 490). Here Newell contrasted the “gradual increase in appreciation of the positive merits of the fossil record” with Darwin’s earlier “preoccupation with the deficiencies in the record,” and while he noted a continued “lively debate” over interpretations of the record, he cited a “general agreement... that many striking patterns of fossil distributions have been confirmed hundreds of times” (Newell, 1959: p. 490-1). In terms of the sheer quantity of paleontological data, Newell pointed to the dramatic improvement of knowledge of the record: whereas Charles Schuchert estimated, in 1910, some 100,000 extant fossil species, Kurt Teichert’s calculation in 1956 raised that number to ten million (Newell 1959: p. 492; (Schuchert, 1910: p. 591-2; Teichert, 1956). Overall, Newell predicted “the future prospects for paleontology are, indeed, very bright if an ample supply of paleontologists can be trained and oriented toward systematic exploration of the fossil record” (Newell, 1959: p. 499).

CONCLUSION

Over the next number of years, paleontologists would confront evidentiary shortcomings in part by developing increasingly sophisticated methods for recognizing and overcoming inevitable ‘biases’ in the fossil record. This kind of study would make analysis and interpretations of broad-scale patterns of evolution and extinction possible, and ultimately led to the quantitative, model-oriented paleobiology practiced by many paleontologists today. For example, it was Simpson who first proposed, in the 1940s, that sequential discontinuities in the fossil record (especially across taxonomic categories) might not always be artifacts of imperfect preservation: “the development of discontinuities between species and genera, and sometimes between still higher categories, so regularly follows one sort of pattern that it is only reasonable to infer that this is normal and that sequences missing from the record would tend to follow much the same

pattern” (Simpson, 1944: p. 98). In fact, Simpson continued, “the face of the fossil record really does suggest normal discontinuity at all levels” (Simpson, 1944: p. 99). While Simpson did not claim (as paleobiologists would often later do) that the fossil record is a mostly complete document, neither did he join in Darwin’s and many fellow paleontologists’ characterization of that record as devoid of theoretical interest. Perhaps his most important message on this topic was that “incompleteness is an essential datum and... can be studied with profit” (Simpson, 1944: p. 105).

Darwin’s dilemma, then, did not ultimately prevent paleontology from taking a place at the evolutionary ‘high table,’ but it did delay its entry considerably. Darwin’s metaphor of the incomplete book exercised a powerful influence on paleontological study of the fossil record for decades after the publication of *Origin of Species*, and produced in some cases an inferiority complex among paleontologists that was difficult to overcome. In a final irony, however, Darwin’s dilemma may, perhaps, have had an unexpected positive effect: the paleobiological movement that arose in the 1950s and which dominates the field today developed, in large part, out of an effort to respond to perceived inadequacies in paleontological data. By developing statistical and empirical techniques to model and extrapolate an inherently fragmentary fossil record, paleobiologists ultimately took their field in a direction that Darwin and other 19th century naturalists could never have imagined. As much as Darwin may have discouraged some paleontologists from applying their tools to evolutionary study, he undoubtedly (and probably unintentionally) inspired others to look for innovative ways to transcend empirical shortcomings. In the final analysis, then, it could be fairly claimed that Darwin’s dilemma proved both a curse and a blessing for the development of modern paleontology.

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