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ORIGINAL RESEARCH

Biased, Spasmodic, and Ridiculously Incomplete: Sequence Stratigraphy and the Emergence of a New Approach to Stratigraphic Complexity in Paleobiology, 1973–1995

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Abstract

This paper examines the emergence of a new approach to stratigraphic complexity, first in geology and then, following its creative appropriation, in paleobiology. The approach was associated with a set of models that together transformed stratigraphic geology in the decades following 1970. These included the influential models of depositional sequences developed by Peter Vail and others at Exxon. Transposed into paleobiology, they gave researchers new resources for studying the incompleteness of the fossil record and for removing biases imposed by the processes of sedimentary accumulation. In addition, they helped reconfigure the cultural landscape of paleobiology, consolidating a growing emphasis on fieldwork and eroding the barrier that had been erected in the 1970s between "paleontology" and "paleobiology." This paper traces these developments, paying special attention to the simulation models of stratigraphic paleobiologist Steven Holland. It also considers how the integration of sequence and event stratigraphy and paleobiology has begun to influence long-running discussions of incompleteness and bias in the fossil record.

Keywords Stratigraphy · Sequence stratigraphy · Paleobiology · Derek Ager · Peter Vail · Steven Holland

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Introduction

In 1995, Stephen Jay Gould issued the last of what his colleagues jokingly described as his "state of paleontology" addresses. The occasion was the twentieth anniversary of *Paleobiology*, the journal that had served as the focus and principal mouthpiece of the paleobiological revolution (Sepkoski 2012).[1] Gould's title was "A task for paleobiology at the threshold of majority [legal adulthood]." The "task" had two components. First, paleobiologists were to characterize "narrative patterns" in the history of life, such as "[the] Mesozoic and Cenozoic trend to greater global species diversity" (Gould 1995, p. 8). Then they were to explain these patterns using a body of home-spun evolutionary theory (Gould 1995, p. 7). Gould was careful to note that theory alone "does not define the task of paleobiology," since "narrative patterns of life's long-term history are as important as theories invoked to explain them." Still, "the twin themes of macroevolutionary theory and [large-scale] pattern work together to define the task of paleobiology for the evolutionary sciences" (Gould, p. 12). And since paleobiology *was* an evolutionary science, these themes came close to exhausting the task of paleobiology as a whole.

Gould's view of paleobiology as organized around large-scale patterns and their explanation has found uptake in recent historical scholarship. An important reason is that this scholarship has focused on the paleobiological revolution and its architects, spanning the interval from about 1970 to 1985. Apropos of this focus, two themes have come to play coordinating roles in the historiography of the field. The first is that paleobiology is a *biological* (read: *evolutionary*) science, which is tasked above all with contributing to *evolutionary theory* (Bambach 2009; Grantham 2009; Ruse 2009; Valentine 2009; Turner 2009, 2011; Baron 2011; Sepkoski 2012, 2013, 2019; Dresow 2017, 2019; Tamborini 2022). The second is that paleobiology is a science centered on the analysis of *large amounts of data* (Sepkoski 2012, 2013, 2017, 2019; Sepkoski and Tamborini 2018; Tamborini 2019). It is not an activity concerned with the classification and interpretation of individual fossils.

Because the historiography of paleobiology has centered on these themes, inquiry has tended to focus on two topics: the drama of paleontology's relationship with evolutionary theory and the history of practices used to characterize and explain large-scale evolutionary patterns. Yet this has left sizable gaps in our understanding, most notably concerning paleobiology's relationship to the *geosciences*. It was no aim of the seventies revolutionaries to alienate paleontology entirely from the geosciences, after all. Even Gould affirmed "the absolute necessity of comprehensive geological training for success in paleontology"—and this in a paper touting paleobiology's promise as an *evolutionary discipline* (Gould 1980, p. 98). "[With] all biology and no geology, paleontology is empty; but with geology alone it is blind."

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[1] The *paleobiological revolution* is the name given to a series of developments that saw the emergence of paleobiology as a distinct area of study "centered around the quantitative analysis and interpretation of the history of life" (Sepkoski 2013, p. 402). It is usually dated from about 1970 to 1985 and associated with American invertebrate paleontologists like Gould (1941–2002), David Raup (1933–2015), J. John (Jack) Sepkoski, Jr. (1948–1999), Steven Stanley (1944–), and Thomas Schopf (1939–1984).

It was blind without biology because paleontology's most important questions came from evolutionary theory, or so Gould tended to suppose. Yet it was empty without geology because in its working methods and visual language, there was much in paleobiology that was distinctively geological.

This paper begins to fill the gap in our understanding of paleobiology as a geoscience. It does this by tracing the emergence of a new approach to stratigraphic complexity, first in geology and then, following its creative appropriation, in paleobiology. The approach was associated with a set of models that together transformed stratigraphic geology in the decades after 1970. These included Derek Ager's model of event deposits, as well as the model of depositional sequences developed by Peter Vail and others.[2] Transposed into paleobiology, these gave researchers tools for studying the incompleteness of the fossil record and for coping with biases imposed by the processes of sedimentary accumulation (Brett 1995, 1998; Holland 1995). They also helped reconfigure the cultural landscape of the discipline, consolidating a growing emphasis on fieldwork and eroding the barrier that Gould and others had erected between the "old" and the "new" paleontology.

The remainder of the paper contains seven sections. "The Paleobiological Revolution and Beyond" examines the strained relationship between paleontology and stratigraphy in the lead-up to the paleobiological revolution, and reviews strategies paleobiologists developed to cope with the incompleteness of the fossil record. This is followed by three sections ("Stratigraphy Before 1970"; "More Gap than Record"; "Sequence Stratigraphy") that trace the development of the "new" stratigraphy, whose creative appropriation would provide another approach to the analysis of the fossil record in the wake of the paleobiological revolution. "The Stratigraphic Distribution of Fossils" examines how sequence stratigraphic models, in particular, were seized upon by paleobiologists, focusing on the simulation studies of "stratigraphic paleobiologist" Steven Holland. "Paleobiology, Prestige, and 'The Field'" considers how studies like Holland's influenced paleobiological attitudes towards "the field" as a site of knowledge production. Finally, the "Conclusion" asks how the integration of stratigraphy and paleobiology has influenced long-running discussions of "incompleteness" and "bias" in the fossil record—discussions that have been a staple of paleontological discourse since the early nineteenth century.

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[2] Sequence stratigraphy has been almost entirely ignored by historians. The only historian who seems to have noticed it is David Oldroyd (2006). However, its influence on stratigraphic practice has been immense. One commenter has gone so far as to compare this influence to that of plate tectonics on structural geology (Mitchum 2003). Doubtless this is an exaggeration, but even more sober commenters agree that its influence has been pervasive: "Modern stratigraphy is dominated by the study of 'sequence stratigraphy'" (Miall and Miall 2002, p. 307). A secondary goal of this paper is therefore to draw attention to this crucial development in the recent history of the earth sciences.

The Paleobiological Revolution and Beyond

The science of paleobiology was founded, in no small part, on a desire to extricate (invertebrate) paleontology from stratigraphic geology. This was necessary, it was argued, so that paleontologists might cultivate a genuinely biological attitude towards their subject matter: the fossilized remains of past organisms. Fossils have a variety of uses in geological research, not the least of which is as tools for subdividing and correlating rock units (Rudwick 1985; Dresow 2021). However, nothing in this practice requires the investigator to regard fossils as the remains of once-living organisms as opposed to neutral markers of stratigraphic position. As such, stratigraphic paleontology, which provided the main employment for invertebrate paleontologists during the twentieth century, failed to develop a pronounced biological orientation (Sepkoski 2012; Rudwick 2017). Its questions tended to be geological and utilitarian, and its practitioners narrow taxonomic specialists as opposed to question-driven biological researchers. J. Brookes Knight (1888–1960), an invertebrate paleontologist, put the point tartly in his 1947 presidential address to the Paleontological Society:

> [What] we today call a paleontologist, particularly that jellylike variety without a backbone, incapable of standing erect on his own two feet, the invertebrate paleontologist, is not a paleontologist at all. He is a geologist, a stratigraphical or ‘soft-rock’ geologist. He has considerable familiarity with invertebrate fossils, to be sure, but he is a geologist nevertheless. (Knight 1947, p. 284)

The problem had evidently not abated by 1968, when Martin Rudwick (1932–), then working as an invertebrate paleontologist, complained that paleontology had been “stunted throughout its existence by its subservience to the needs of stratigraphy”:

> This [subservience] has hindered the mainstream of paleontological work from developing any genuinely biological attitude. The situation has certainly improved within the last decade, but even today what is so often missing is any imaginative awareness of fossils as the remains of organisms that were once alive. (Rudwick 1968, p. 35)

Even in 1980, paleobiologists continued to press this narrative:

> Invertebrate paleontology has cast its institutional allegiance with geology—more by historical accident than by current logic. When it operates as a geological discipline, paleontology has tended to be an empirical tool for stratigraphic ordering and environmental reconstruction. As a service industry, its practitioners have been schooled as minutely detailed, but restricted experts in the niceties of taxonomy for particular groups in particular times. (Gould 1980, p. 98)

All this pointed to a consensus among would-be paleobiologists: (1) that the science of (invertebrate) paleontology had been unjustly subordinated to stratigraphy; (2) that progress in paleontology required the cultivation of a genuinely biological attitude; and (3) that because the subordination of paleontology prevented the cultivation of this attitude, the future of paleontology hinged on its separation from stratigraphy, as well as the reassertion of its status as an autonomous biological science.[3]

But how was this to be achieved? Gould, at least, had a plan. If paleontology were to slip the yoke of stratigraphy and assert its autonomy as a biological science, it needed to cultivate a new attitude toward its data, on the one hand, and towards evolutionary theory, on the other (Gould and Eldredge 1977; Gould 1980). This involved breaking a loop of mutual reinforcement that saw paleontology relegated to the margins of evolutionary science: to a source of data about life's empirical pattern, but not a contributor of new ideas. For Gould, it all began with the fossil record. Since the middle of the nineteenth century it had been a commonplace that the record of the rocks is woefully incomplete. Charles Darwin referred to it as "a history of the world imperfectly kept," and proceeded to deny that we have any 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" (Darwin 1859, pp. 310, 301). Later paleontologists mostly agreed with this assessment (Sepkoski 2012, pp. 12–17). It was not the case that here and there in the pile of formations a page was missing from the record book of Earth history. On the contrary, the record was missing *most* of its pages, and those that remained were torn and blotted, or else covered in confused writing like a palimpsest. It was this dim view of the fossil record that Gould and others sought to reform "through a deliberate manipulation of Darwin's book metaphor" (Sepkoski 2012, p. 3). If the fossil record were a text, then the strategy of paleobiologists would be to "reread" it in a way that enabled them to reach general conclusions about the history of life.

Sepkoski identified three strategies that 1970s-era paleobiologists developed to reread the fossil record (Sepkoski 2012). The first he termed *literal rereading*, and consisted in a willingness to interpret certain patterns in the record, at least, as trustworthy signals. So Eldredge and Gould (1972, p. 96) wrote that "[m]any breaks in the fossil record are real; they express the way in which evolution occurs, not the fragments of an imperfect record." This amounted to a denial that Darwinian pessimism was an obligatory attitude towards all aspects of the fossil record. But just how far literalism could take you was anyone's guess. By contrast, the second strategy doubled down on pessimism. Inspired by abstract modeling practices in ecology, *idealized rereading* aimed to circumvent the messiness of the record by simulating the history of life *in silico*. In these simulations, "the physical particulars of the fossil record [were] all but ignored, and the history of life… [was] modeled as a series of homogeneous data points… using very simple parameters" (Sepkoski 2012, pp. 3–4). The results of the simulations could then be compared against the fossil record

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[3] Similar criticisms were voiced by German-speaking paleontologists prior to World War Two (Rieppel 2013). A leading figure, the Austrian paleontologist and National Socialist Othenio Abel (1875–1946), even spoke of "the battle to free paleontology from the shackles of geology" (Abel 1929, p. 153), although there is little evidence to suggest that the paleobiology of the 1970s was directly influenced by Abel's *Paläobiologie*.

to see how well they recovered empirical patterns. Finally, there was the approach Sepkoski called *generalized rereading*, which involved the stockpiling of data in large electronic databases for the purpose of framing "statistical generalizations… about patterns in life's history" (Sepkoski 2012, p. 4). This involved "meticulous collection of data on a monumental scale and [the] interplay between mathematical modeling and rigorous, insightful data analysis" (Foote 1999, p. 326). So, instead of an attempt to smooth over the incompleteness of the fossil record with copious data, generalized rereading hinged on the practice Alisa Bokulich has described as "models correcting data" (Bokulich 2018).

As Sepkoski observed, generalized rereading would go on to become the dominant methodology in analytical paleobiology and remains an important feature of paleobiological practice to this day (Sepkoski 2012). Yet generalized rereading was most easily applied to studies at the largest spatial and temporal scales, like global surveys of marine taxonomic diversity through time. For studies of individual basins, not to mention bed-by-bed studies of morphological or ecological change, other strategies were more applicable, like literal rereading. But literal rereading had serious limitations, as even Gould was fast to admit (Gould 1969). To name just one, it was evident that the pattern of fossil occurrences in outcrops were shaped by factors ranging from the differential supply of sediments to the tectonic history of basins (Sadler 1981; MacLeod 1991). A strategy was thus needed for unscrambling these biases: for extracting biological signals from the distorting effects of stratigraphic overprint. It is my claim that researchers eventually found this in the "new" stratigraphy, but only after a new generation of paleobiologists had traversed the cultural gap that had opened between paleobiology and stratigraphy during the paleobiological revolution.

The next three sections examine the roots of this strategy by exploring developments in stratigraphy that made possible a fruitful reconciliation with paleobiology after the paleobiological revolution. "Stratigraphy Before 1970" explores the background to the major changes in stratigraphic practice that took place during the 1970s. Then the sections titled, "More Gap Than Record" and "Sequence Stratigraphy" unpack these changes, and introduce the new model of the stratigraphic record that emerged in their wake.

Stratigraphy Before 1970: From the Layer Cake to the Crazy-Quilt

Stratigraphy is the study of layered sediments, and layered sediments are the major archive of geohistory: "the sum of a thousand narratives in stone-stacked order" (Fortey 1997, p. 8). A major goal of geology is to piece together these narratives from scattered evidence and to fit them into appropriate spatial and temporal frameworks (the tasks of reconstruction and correlation, respectively). Since the beginning of the nineteenth century, geologists have labored "to name and measure every stratum of every sequence on earth, to detail its component minerals, and to reconstruct the story of its formation, its existence, and in many cases its deformation and destruction" (Greene 2009, p. 171). This activity is basically stratigraphic. Elaborate reconstructions of geohistory are built upon the frameworks supplied by stratigraphy; so in this significant sense, stratigraphy provides "the key to understand[ing] the Earth, its… structure and past life" (Doyle and Bennett 1998, p. 1).

Central to stratigraphy throughout its long history has been paleontology, since fossils provide a useful way of correlating rocks over hundreds, or even thousands, of kilometers (Rudwick 1985). Enthusiasm for this practice blossomed during the nineteenth century when it was recognized that many systems established on the basis of fossil evidence could be recognized abroad, even on different continents. Guided by the fossil record, geologists were able to see past "the bewildering variety of local formations and the confusing effects of local tectonic disturbances" to articulate a consistent outline of geohistory for the largest divisions of geological time (Rudwick 1972, p. 199). With the refinement of stratigraphic methods, hopes were high that the geological column might be decomposed into a predictable succession of *zones* with global, or near-global, applicability. The rock record might then be pictured as a kind of layer cake, with each layer representing a unique interval of time as well as a group of strata formed during that interval.[4]

Although many nineteenth century geologists held views that later generations would characterize as "layer cake stratigraphy," most were aware that the stratigraphic record is complex, and that this complexity has an important spatial dimension. In the present day, environmental conditions are highly variable from place to place. Even at a single location, a variety of environments may be found in close proximity, each with its own complement of biological inhabitants. Conditions in the past were likely similar, at least in the sense that many environments are likely to have existed side by side, forming a mosaic of environmental conditions. It is therefore expected that this mosaic will be reflected in the rocks as a mosaic of lithological and paleontological characteristics. As the first director of the Geological Survey of Great Britain, Henry De la Beche, wrote in 1839, it is most unlikely "that detrital matter has been strewed in exactly the same manner, enveloping exactly the same organic remains, over all parts of the world, where deposits were taking place at the same time" (p. 39). His point was directed against those who assumed a contrary picture in their practice: in particular, those who assumed that the rock record could be analyzed as a stack of mostly homogeneous strata, each enclosing a distinctive set of fossils that fixed its position uniquely in the pile.

The term *facies* was introduced in 1838 and signaled an increased recognition that the characteristics of a rock unit can vary considerably from place to place (Rudwick 2008, pp. 457–460).[5] Yet the notion that the record resembles a layer cake—one with dappled layers, perhaps, but a layer cake nonetheless—persisted into the twentieth century (Brown 2013). Especially in North America, stratigraphers continued to describe strata as laterally extensive sheets of mostly homogeneous rock, with the

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[4] Along with exhibiting this temporal pattern, many stratigraphers expected the rock record to resemble a layer cake in its physical structure as well. This is a more literal, and nowadays universally condemned, application of the layer cake metaphor.

[5] *Facies* is a Latin word meaning "face" or "external appearance" (Teichert 1958). In geological usage, it means a sedimentary deposit characterized by a set of features that formed in a particular depositional environment, like a coastal plain or reef front.

presumption that these corresponded to unique intervals of geological time. These stratigraphers knew that lithologies often shift as you trace a formation laterally: the phenomenon of lateral facies change (Brett et al. 2007). They also knew that rock units of consistent lithology were not necessarily *isochronous*, or equivalent in age over their entire geographical spread. Still, stratigraphers in the early twentieth century remained preoccupied with the task of mapping broad packages of strata over wide geographical areas, and for this project, layer cake views served passably well. The stratigraphic record may not resemble a perfect layer cake, but it resembles one well enough that geologists could get on with the project of delimiting major packages of strata and correlating them between locations using fossil and lithological indicators. All that is required is that laterally continuous strata exhibit some degree of isochrony: in other words, that units traceable across country not differ markedly in age from place to place. Rock units that differ in age from place to place are called *diachronous*.

The history of stratigraphy in the mid-twentieth century was a story of the erosion of confidence in lateral continuity. Indeed, by the 1960s, the influential stratigrapher Alan B. Shaw could speak of "the universality of diachronism": that is, of the idea that all sedimentary rocks deposited in stratigraphically important environments are diachronous (Shaw 1964, p. x). According to this view, similar-looking and ostensibly continuous strata observed at different locations should not be treated as if they are equivalent in age. Instead, they should be regarded as merely analogous facies and therefore as probably diachronous (Ager 1973).[6] Likewise, faunal occurrences should be interpreted as diachronous unless members of the fauna belong to widespread and short-lived taxa, termed *index fossils* for their usefulness in telling time. By the 1970s, the majority of stratigraphic complexity was analyzed in facies terms and little attention was given to the project of tracing large packages of strata over wide areas (Brett et al. 2007; Miall 2010). As a consequence, paleontological methods began to be regarded with suspicion among the rising class of North American lithostratigraphers, although they continued to find employment in the rapidly expanding field of hydrocarbon exploration (Newell 1962; Shaw 1964).[7]

These developments heralded significant changes in stratigraphy. Out was the practice of tracing continuous strata over large areas, mostly on the strength of fossil evidence. Out too was the practice of representing these strata as uniform blankets bounded by vertical lines which were—echoes of the old layer cake view. In their place was substituted detailed studies of local units and diagrams showing

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[6] As the paleontologist and stratigrapher Carlton Brett (1952–) summarized this view, "if a rock unit looks the same in two different places it must be of different ages" (Brett 2000, p. 496).

[7] The middle of the twentieth century was an exceedingly complicated time in the history of stratigraphy, which saw the consolidation of "pure" lithostratigraphy (the project of delineating and correlating rock units based entirely on lithological characteristics) as well as the expansion of petrography and process sedimentology (Seibold and Seibold 2002; Steel and Milliken 2013). (*Petrography* refers to the descriptive study of rocks, especially under the microscope, whereas *process sedimentology* refers to the actualistic study of sedimentary bodies and structures.) This section outlines developments in lithostratigraphy to the neglect of these other critical areas (but see Dott 1978 for a complementary account).

crazy-quilt patchworks of lithostratigraphic blobs (diachronous facies units). Developments in nomenclature consolidated the trend, calling for a separation of units based on lithology (the subject matter of *lithostratigraphy*), fossils (*biostratigraphy*), and time (*chronostratigraphy*). These developments were generally well received and put an end to the time when a single term might stand-in for a rock unit, a time unit, or some confused hybrid of the two. Still, the growing emphasis on lithostratigraphy added greatly to the complexity of geological nomenclature, as names for local rock units accumulated with increasing rapidity (Bhattacharya and Abreu 2016). In addition, the separation of time and rock units diverted attention away from the study of how time is stored in rocks or in the surfaces separating sedimentary deposits. This would later be lamented. As Carlton Brett put it, looking back from the vantage afforded by the "new" stratigraphy: "[in] their adherence to a stratigraphic code stating that rock units must be kept strictly separate from time units, lithostratigraphers almost lost the most critical of all notions: the perspective of the temporal scope of rock layers" (Brett 2000, p. 496) (Fig. 1).

The eclipse of time in stratigraphy would be a temporary one, and in the next two sections I will examine several ways that mainstream stratigraphers regained an interest in the temporal scope of rock layers. Before coming to this, however, it is worth considering why the alienation of litho- and biostratigraphy resulted in a curiously ahistorical stratigraphy. For much of the history of geology, fossils provided the primary means of determining the temporal relationships of rocks. Although radioisotopic methods were known from the early twentieth century, most rocks could not be dated using isotopes, and other methods lacked the resolving power of biostratigraphy. When lithostratigraphers came to question the usefulness of paleontological techniques, then, biostratigraphy and chronostratigraphy were effectively the same project.[8] It follows that in distancing themselves from paleontological methods, the mainstream of (litho)stratigraphic research lost its best means of establishing time scales for the smaller divisions of geological time (Shaw 1964). It is this alienation that is in focus for complaints that stratigraphy got "sidetracked" in the 1960s and "lost… the perspective of the temporal scope of rock layers."

There is an irony in all this: that, while paleontologists were bemoaning their subordination to stratigraphy, paleontological methods were in the process of being expelled from much stratigraphic research.[9] However, it would not be long before geologists were reminded of the temporal scope of rock layers. And perhaps unsurprisingly, it would be a paleontologist who would do the reminding.

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[8] This is not to say that biostratigraphic (rock) units were ever explicitly defined as chronostratigraphic (time) units, although in practice they were frequently treated as such (Hedberg 1965). It is just to say that, in the mid-twentieth century, fossils provided the key line of evidence for chronostratigraphic dating.

[9] For example, here is the "grandfather" of American paleobiology, Norman Newell (1919–2004), writing in 1962: "As stratigraphic work in the United States has been increasingly directed to local and minor stratigraphic units there has been a growing emphasis on physical criteria and less attention to fossils… This decline in stratigraphic paleontology has resulted in widespread lack of appreciation of fossils as indices of time and environment, and many stratigraphers relegate fossils to a minor role in classifying and correlating strata" (Newell 1962, p. 592). Ironically, Newell had earlier been keen to articulate worries about the subordination of (invertebrate) paleontology to stratigraphy (Sepkoski 2012, pp. 57–59).

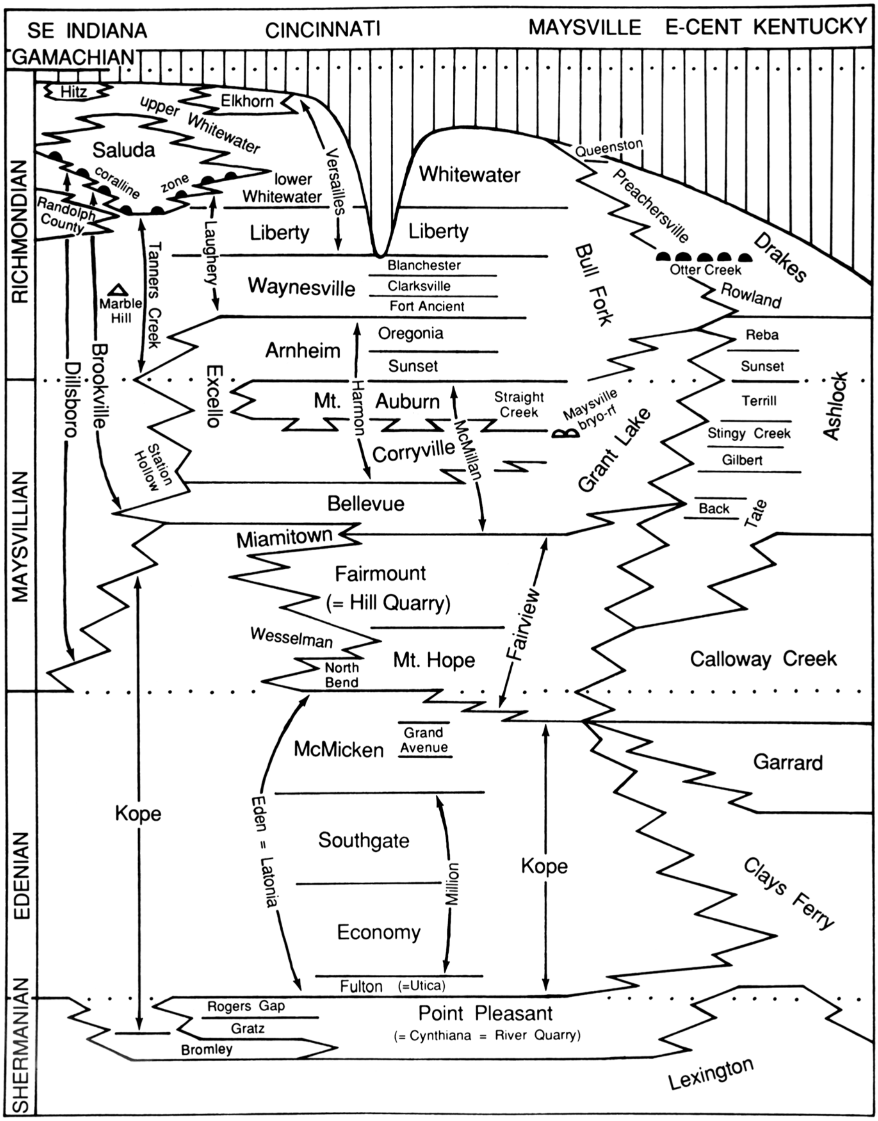

Fig. 1 A diagram of the Cincinnatian strata of Indiana, Ohio, and Kentucky, showing lateral relationships between diachronous facies units (Cuffey 1998, Fig. 2.3; by permission of the ODNR Division of Geological Survey). Here, geographical area is represented on the horizontal axis, and time on the vertical. This representation of the rock record shows problems with the layer cake view

"More Gap Than Record"

"There is something damn funny about the stratigraphical record." So wrote Derek Ager (1923–1993) in a volume whose slim dimensions belie its enormous importance in the history of stratigraphy (Ager 1973, p. 1). Ager was a paleontologist, and

The Nature of the Stratigraphical Record was an "ideas book," all of which might have been expected to blunt its impact in the detail-oriented field of stratigraphic geology. However, as the stratigrapher Andrew Miall (1944–) recalled, "the issue of time in stratigraphy did not begin to have a major influence on the science until Ager's work in the 1970s" (Miall 2015, p. 285). In this section, I will examine a few of the central ideas from *The Nature of the Stratigraphical Record*, including the rapidity of much sedimentation and the ubiquity of gaps in the geological column. Together these constituted a bracing critique of traditional thinking in stratigraphy, and one that pointed to a view of the stratigraphic record as both more dynamic and more incomplete than past stratigraphers had envisioned.

What did Ager find so damn funny about the "stratigraphical record"? For one thing, "[the] record is spasmodic and ridiculously incomplete, with particular strata and fossils extremely widespread, but separated by vastly longer gaps than anything that is preserved" (Ager 1973, p. 75). For another, individual strata and fossils are almost certainly diachronous (Ager agreed with Shaw that most sedimentary units and fossils spread out diachronously, with the possible exception of deep-sea oozes). However, because the record is "ridiculously incomplete," these strata and fossils are "to all intents and geological purposes *synchronous*" (Ager 1973, p. 75, emphasis added). It is not the case that diachronism destroys the value of fossils and sedimentary bodies as markers of time. As unlikely as it might have seemed in 1973, the chronostratigraphic layer cake had some fizz in it still.[10]

In Ager's view, one of the chief results of "Recent sedimentary studies… has been the demonstration of lateral rather than vertical sedimentation" (Ager 1973, p. 51). "Modern deposits are not, it seems, laid down layer upon layer over a wide area" as old-fashioned layer cake stratigraphers imagined (Ager 1973, p. 52). Rather, "[they] start from a particular point and then build out sideways as in the traditional picture of a delta." To illustrate the point, Ager offered the analogy of "carpets being brought periodically into a shop for display and rolled out one by one on a pile" (Ager 1973, p. 75). The end product of this stacking would resemble a kind of layer cake with distinct carpet-layers piled on top of each other. Still, "the process of formation and the record it preserves" would be very different from those envisioned by nineteenth century geologists. First, "we know that the time-gaps between successive layers might have been very considerable"—an issue for any view that assumes that most time is stored in sediments as opposed to surfaces. Second, "[we] know that when a new layer arrived, it was not deposited simultaneously all over the preceding layer" (Ager 1973, p. 75). This means that diachronism really is universal, although perhaps not in a way that destroys the temporal value of rock layers (more on this shortly).

Ager's most important insight, though, was not his insistence that sedimentation consisted in lateral spreading rather than vertical stacking. Instead, it was his claim that significant portions of the geological record were deposited in a very short time by "catastrophic events" like hurricanes and underwater avalanches. These events

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[10] Again, the chronostratigraphic layer cake should be distinguished from the view that the rock record *physically* resembles a layer cake. The latter analogy, Ager thought, "just will not do" (Ager 1973, p. 75).

were geologically instantaneous—unlike the deposits discussed in the previous paragraphs—and some were extremely widespread. As a consequence, they were potentially useful for high-resolution correlation and chronostratigraphic analysis, even over large geographical areas.

> We have managed to confuse ourselves for years with the jargon of lithostratigraphy, biostratigraphy, chronostratigraphy and the rest. In fact, it can be argued that basically there are only two concepts—rocks and time—with the rest just an obfuscation of nomenclature. Nevertheless … I make no apology for suggesting another term, just to draw attention to its usefulness as a method. This is what may be called 'event stratigraphy' in which we correlate not the rocks themselves, on their intrinsic petrological characters, nor the fossils, but [discrete geological and biological] events. (Ager 1973, pp. 62–63)

The term "[high-resolution] event stratigraphy" has since passed into general usage; likewise the practice of constructing high-resolution time scales on the basis of "geologically instantaneous" events (Aigner 1985; Kauffman 1988; Cramer et al. 2015).[11] According to Patzkowsky and Holland (2012), it is one of two approaches that lies at the heart of "stratigraphic paleobiology," since it permits the correlation of individual beds and bed sets: a prerequisite for resolving the dynamics of paleobiological events in single sedimentary environments (Holland 1999, 2000). The other approach is sequence stratigraphy, the subject of the next section.

There is a flip side to the view that most sedimentation is episodic, and that large portions of the geological record accumulate in virtually instantaneous events. This is the view that the record is gappy—"more gap than record," in Ager's expression—*even in putatively complete sections*. Ager noted that the traditional way of representing the stratigraphic column is as a stack of rocks interrupted, if at all, by minor gaps (Fig. 2). However, a "far more accurate picture" is that of a single long gap "with only very occasional sedimentation" (Ager 1973, p. 35).

> Perhaps the best way to convey this [picture] is to remember a child's definition of a net as a lot of holes tied together with string. The stratigraphical record is a lot of gaps tied together with sediment. It is as though one has a newspaper delivered only for the football results on Sunday and assumes that nothing at all happened on the other days. (Ager 1973, p. 35)

As Ager observed in a later book, each bedding plane is effectively an unconformity: a surface corresponding to a period of non-deposition and erosion (Ager 1993). And the number of bedding planes in a stratigraphic succession is likely to be enormous. The upshot is that "gaps probably cover most of earth history, not the dirt that happened to accumulate in the moments in between" (Ager 1993, p. 14). Or as he wrote in the oft-quoted conclusion to *The Nature of the Stratigraphical Record*: "the

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[11] These *event beds* have been likened to frosting layers in a well-marbled cake (Brett 2000). The implication is that even if the cake layers (local facies) are diachronous, stratigraphers can still use the frosting layers to divide the cake into roughly time-parallel units.

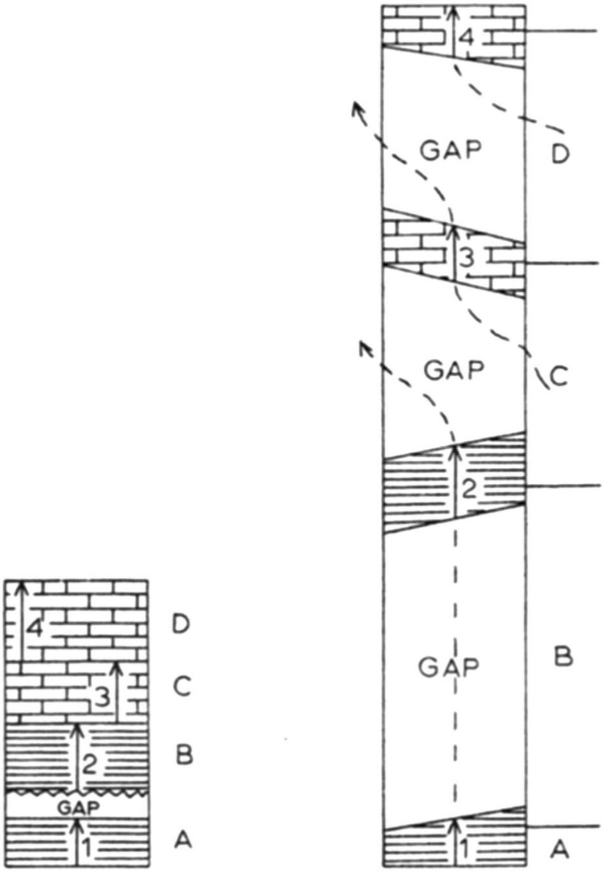

Fig. 2 A comparison of a conventional representation of a stratigraphic column (left) with "what is probably the true picture" (right) (Ager 1973, Text-Fig. 3.4; by permission of John Wiley & Sons). Notice that in the "probably… true picture," strata are represented as diachronous (titled), in accordance with Ager's view that sedimentation consists in lateral spreading as opposed to "gentle rain from heaven" (Ager 1973, p. 33). The arrows in the diagrams represent assumptions about fossils, and can be ignored for the purposes of this discussion

history of any one part of the earth, like the life of a soldier, consists of long periods of boredom and short periods of terror" (Ager 1973, p. 100).

Ager's work had an immediate impact on stratigraphic thinking. Apart from stimulating interest in "catastrophic" events, probably the most important thing it did was reopen the question of the temporal scope of rock layers, and increasingly of surfaces corresponding to gaps in the record. Time is continuous, but sedimentation (and therefore the stratigraphic record of time) is not. However, to understand the distribution of gaps in the record, geologists need tools for parsing controls on sedimentary accumulation on a range of spatial and temporal scales. These were mostly unavailable when *The Nature of the Stratigraphical Record* appeared in

1973. However, they were soon to become available with the introduction of a new approach to stratigraphic complexity for larger scales of time.

Sequence Stratigraphy

The basic ideas behind sequence stratigraphy began to coalesce in the 1940s, but it was not until the 1980s that they began to exert a sizable influence on stratigraphic practice (Sloss 1988). The main author of this influence was Peter Vail (1930–), a stratigrapher working for Exxon's Upstream Research Group (formerly the Esso Production Research Company). But it was Vail's doctoral advisor, Laurence Sloss (1913–1996), who got the ball rolling with his study of the enormous packages of strata comprising the cratonic region of North America.[12] Sloss was an outlier among mid-twentieth century lithostratigraphers. While many of his colleagues were engaged in describing local stratigraphic units, Sloss was interested in a scale of analysis encompassing whole basins, and indeed multiple basins linked by correlation (Sloss 1988). Sloss was also unusual for his interest in external controls on sedimentary processes—things like tectonism and sea-level change—as opposed to processes internal to sedimentary systems. He speculated in 1949 that the North American craton contained four major "unconformity-bounded successions," which were controlled by tectonic events (Sloss et al. 1949). When the crust went down, shallow seas invaded the continental interior and sediment was deposited. When it went up, the seas retreated and exposed previously deposited sediments to erosion. Later, Sloss demonstrated an association between these "sequences" (the number had since grown to six) and major rises and falls in sea-level, suggesting that global sea-level exerts a first-order control on sediment accumulation (Sloss 1963). It was observations like this that set the agenda for future studies of depositional sequences, including Vail's work at Esso and, later, Exxon.

Vail's early work in the petroleum industry was aimed at developing, applying, and evaluating new mapping techniques for hydrocarbon exploration (Vail 1992; Oldroyd 2006). This was standard fare for an economic geologist trained in the 1950s. However, when high-quality seismic reflection data became available around 1960 (largely in virtue of advances in computer processing), Vail decided to switch tracks.[13] Oil companies had begun to use seismology to map underground relationships several decades earlier, with the objective of locating valuable hydrocarbon

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[12] A *craton* is a large and ancient block of crust that comprises the nucleus of a continent (Kay 1974). *Cratonic regions* are the regions overlying cratons, which contain piles of younger rocks. What Sloss and colleagues showed was that the cratonic region of North America could be subdivided into four "unconformity-bounded successions": thick packages of strata inferred to have a shared origin in tectonic movements (Sloss et al. 1949). This number was later increased to six in a paper that many regard as the earliest example of the modern "sequence" concept in action (Sloss 1963; see also Sloss 1988).

[13] Seismic reflection data is often presented in the form of *seismic [reflection] profiles*: visualizations of reflected acoustic energy that picture subsurface structures to depths of tens of kilometers. The innovation that stimulated Vail's interest was the ability of computer-aided reflection seismology to image subsurface stratification patterns at high levels of resolution (Sloss 1988; see also Oldroyd 2006, pp. 146–147).

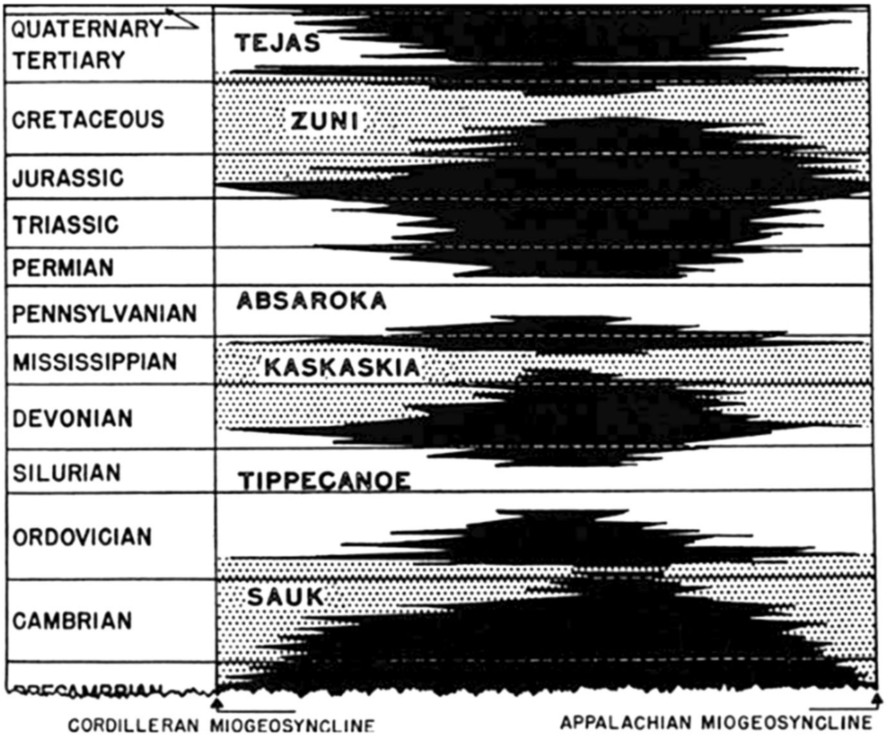

Fig. 3 The six North American sequences identified by Sloss (1963, Text-Fig. 6; by permission of the Geological Society of America). Here space is plotted on the horizontal axis and time on the vertical. Rocks are represented by white or stippled wedges, while non-depositional hiatuses are represented in black. The alternation of white and stippled patterns is a device to enhance readability. Changes in stippling mark changes in sequences; they have no lithological significance. Each sequence is bounded by a major regional unconformity (or non-depositional surface) without specific time significance

reserves without costly drilling. But the practice was notoriously unreliable, and remained so even as higher-resolution reflection profiles became available. In Portuguese Guinea, for example, Vail was tasked with examining a series of three wells, the first of which had been drilled into "a major Cretaceous reservoir of sand, overlying an unconformity with Paleozoic rocks below" (Vail 1992, p. 86).[14] The top of the sand layer corresponded to a reflection surface (a line on a seismic profile), and since it was assumed that seismic reflections were generated by changes in lithology, it was expected that a second well would encounter sand at the same level as the first. Yet when a second well was drilled it encountered sand two reflection layers *lower* than the first well. A third well encountered sand at even greater depth. This seemed to indicate that whatever was generating reflection surfaces, it was not changes in lithology associated with facies boundaries (Vail et al. 1977a, pp. 100–102).

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[14] This work took place in the 1961.

The breakthrough came when Vail recruited a paleontologist, Lou Stover, to date the sand and reflection layers using biostratigraphy. This seemed to indicate that the reflection surfaces—not the sand layers—were equivalent in age. Vail's earlier work had shown that physical surfaces in rocks often "cross the facies of time-transgressive rock units" (Vail 1992, p. 87). Stover's dates were consistent with this view. This led Vail to conclude that the surfaces on reflection profiles correspond to isochronous physical surfaces (bedding planes) as opposed to diachronous facies boundaries (Vail et al. 1977a). Far from "a low-resolution tool for mapping major rock units [facies]," reflection seismology seemed to be "a high-resolution tool for determining [the relative ages of rocks]" (Vail 1992, p. 87).[15]

The realization that seismic records could be used to decipher the history of sedimentary basins was a fruitful one. Using Exxon's wealth of proprietary data, Vail's team set to work developing the approach to make regional chronostratigraphic correlations and, more ambitiously, to construct interpretive diagrams depicting global sea-level change through time (Miall and Miall 2001, 2002).[16] Their important publication appeared in 1977 and is commonly cited as AAPG Memoir 26 (although its full name is *Seismic Stratigraphy—Its Application to Hydrocarbon Exploration*).[17] In it, Vail and colleagues argued that the stratigraphic record of continental shelf deposits consisted of a series of stratal packages partially bounded by unconformities: "depositional sequences" (Mitchum et al. 1977).[18] Since unconformities and their correlative conformities appeared as lines on seismic profiles, geologists could use these profiles to recognize sequences throughout a basin, or in several basins linked by correlation. This would enable them to understand the structure of basins in terms of processes responsible for major features of that structure. In addition, since sequences included chronostratigraphically significant surfaces, sequence analysis promised what J.C. Van Wagoner and colleagues described as "a powerful methodology for the analysis of time and rock relationships in sedimentary strata"—one that blurred the line between chrono- and lithostratigraphy and reopened

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[15] The extent to which seismic reflectors correspond to chronostratigraphic horizons became an object of controversy in subsequent decades. The most acute point of controversy concerned whether depositional sequences are indeed "geochronologic units" with potentially global validity (Vail et al. 1977b, p. 96). Vail and colleagues argued that they are, and used the postulate of globally synchronous sequence boundaries to construct sea-level curves as a template for dating and correlation (Vail 1977b, c). Critics raised a host of objections: for example, that this application of the sequence model gives too little weight to factors other than global sea-level change in generating sedimentary cycles (Miall 1992; Poulsen et al. 1998). Significantly for the present account, these critics were largely agreed about the utility of the sequence model itself. What they objected to was the notion that sequences are produced by glacially-controlled changes in sea-level, and that this makes them globally correlable (Dewey and Pitman 1998; Dickinson 2003).

[16] Both these applications were ultimately geared toward providing a global framework for petroleum exploration, which would reduce costs from exploratory drilling and increase production profits.

[17] AAPG stands for the American Association of Petroleum Geologists. AAPG Memoir 26 is a collection of twenty-four papers given at a 1975 APPG research symposium, including a series of eleven papers authored by Vail and colleagues on the stratigraphic interpretation of reflection records. For an analysis of its reception and rapid uptake by corporate and academic geologists, see Miall and Miall (2002).

[18] These sequences are considerably smaller than the continent-scale sequences described by Sloss.

questions about what controled the distribution of gaps and sedimentary environments in the rock record (Van Wagoner et al. 1988, p. 44).[19]

Sequence stratigraphy is notorious for its difficult terminology and steep learning curve, but the basics of the approach can be summarized simply enough. In Andrew Miall's formulation, it is the study of "repetitive cycles of [sediment] accumulation followed by [gaps], at various time scales" (Miall 2015, p. 295). Just as important, it is a framework for interpreting the stratigraphic record in terms of a small number of variables, including rates of global (*eustatic*) sea-level change, tectonic subsidence, and sediment supply (Christie-Blick and Driscoll 1995). These parameters are related, with tectonism and sea-level change controlling the space available for sedimentation (termed *accommodation*), and changes in accommodation controlling the accumulation of sediment over tens of thousands to millions of years.[20] (On shorter time scales, sediment accumulation is dominated by the depositional events Ager described as "catastrophic.")

Changes in accommodation also influence the distribution of gaps in the record. According to sequence stratigraphy, when the rate of sediment supply exceeds the rate of increase in accommodation, sediment accumulates, forming packages of sediment called *parasequences*.[21] These are successions of relatively conformable strata bounded at their tops by "flooding surfaces" associated with deepening events (often periods of nondeposition). Parasequences are produced by oscillations in the balance between sediment supply and accommodation; but these oscillations are superimposed on longer-term changes that build the major features of depositional sequences (Fig. 3). The most important of these features are called *systems tracts* and consist of sets of parasequences bounded by surfaces of various kinds. The names of the systems tracts are not important here, but what *is* important is that they succeed one another in regular order and are topped by a *sequence boundary*. This is the surface that separates one depositional sequence from another, and forms when falling sea-level permits the erosion of exposed deposits.[22]

So, sequence stratigraphy is informative about the nature and distribution of gaps in the rock record. But it is also informative about facies relationships. Consider

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[19] To say that a surface is *chronostratigraphically significant* is to say that all the rocks overlying it are everywhere younger than all the rocks underlying it (which is different from saying that the surface is isochronous, or that it represents a time line). Because of this, chronostratigraphically significant surfaces are often used in local correlation.

[20] More precisely, *accommodation [space]* is defined as the vertical envelope between the sea surface and the basement of rocks beneath the sedimentary pile, which is available for sedimentation (Jervey 1988). Changes in accommodation reflect the sum of changes in eustatic sea-level change and tectonism, with rising seas and tectonic subsidence increasing accommodation, and falling seas and tectonic elevation decreasing accommodation.

[21] A typical parasequence is between one and ten meters thick and represents tens to hundreds of thousands of years of elapsed time. By contrast, depositional sequences tend to be thicker (comprising multiple stacked parasequences) and represent millions of years of elapsed time (but see Christie-Blick and Driscoll 1995 for complications).

[22] Sequence boundaries typically represent significant periods of time in which no sediment accumulates. But they are not the only chronostratigraphically significant surfaces in a sequence, and other surfaces, like the *maximum flooding surface*, are also associated with periods of highly reduced deposition.

parasequences. Each parasequence records the seaward movement of a shoreline. This means that if one examines a parasequence in cross-section, the facies within the succession will represent progressively shallower environments as one moves from the bottom of the succession to the top (until one reaches the flooding surface, at which point a deep water facies will give way to a shallow water one). But there are patterns at larger scales too. Parasequences typically occur in groups or *sets* that display consistent trends in their component facies and three-dimensional arrangement (Van Wagoner et al. 1988). The most conspicuous of these trends are stacking patterns, which, together with particular boundaries and the overall position of the set in the sequence, are used to define systems tracts (Mitchum and Van Wagoner 1991). Depositional facies are in turn associated with particular stratigraphic positions, which reflect the sedimentological response to changes in sea-level, sediment supply, accommodation, and other factors (see Fig. 4). As a consequence, sequence analysis can be used to predict the distribution of lithologies in basins—something that can help make sense of the apparently crazy-quilt pattern of sedimentary deposits in a range of stratigraphic systems.

The introduction of sequence analysis had far-reaching effects on geological practice (Kerr 1980; Miall and Miall 2001; Oldroyd 2006).[23] Perhaps the most important thing it did was transform the oil and gas industries, enabling geologists to predict stratigraphic relationships in areas that had yet to be explored by costly drilling (Miall and Miall 2002). But the approach had some more academic consequences as well, including that it: (1) "[raised] questions about [sea-level change] and tectonics that had largely been forgotten in the desire… to explain everything as just so much facies shifting"; (2) "[recognized] genetic units… that have meaning in the interpretation of earth's history"; (3) "[emphasized] the incompleteness of the record and [opened] up the study of surfaces"; and (4) "[raised] questions about sediment accumulation… and about secular trends in the nature of sediment accumulation" (Holland 1999, p. 412). It was these consequences that established the relevance of sequence stratigraphy for paleobiological research beginning in the 1980s. However, it was not until the 1990s that the union between paleobiology and sequence stratigraphy began to take more definite shape, catalyzed by novel applications of sequence models to problems of stratigraphic incompleteness and bias.

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[23] This is no place to review the development of sequence models since the 1970s. Suffice it to say that the basic model of Vail and others was repeatedly amended as higher-resolution seismic data became available, and as the importance of factors beyond eustatic sea-level change became more widely accepted (Miall and Miall 2001; Embry et al. 2007). A major development was the ability to apply sequence stratigraphy directly to outcrops and well-logs in the absence of seismic reflection data (Van Wagoner et al. 1990). Also important was the development of numerical models of sedimentary accumulation, which helped to clarify the internal structure of sequences and the meaning of key surfaces (Jervey 1988; see also Posamentier and Vail 1988; Van Wagoner et al. 1988). All this was crucial in fashioning sequence stratigraphy into "an entirely new way of practicing [stratigraphic geology]" (Miall and Miall 2001, p. 322).

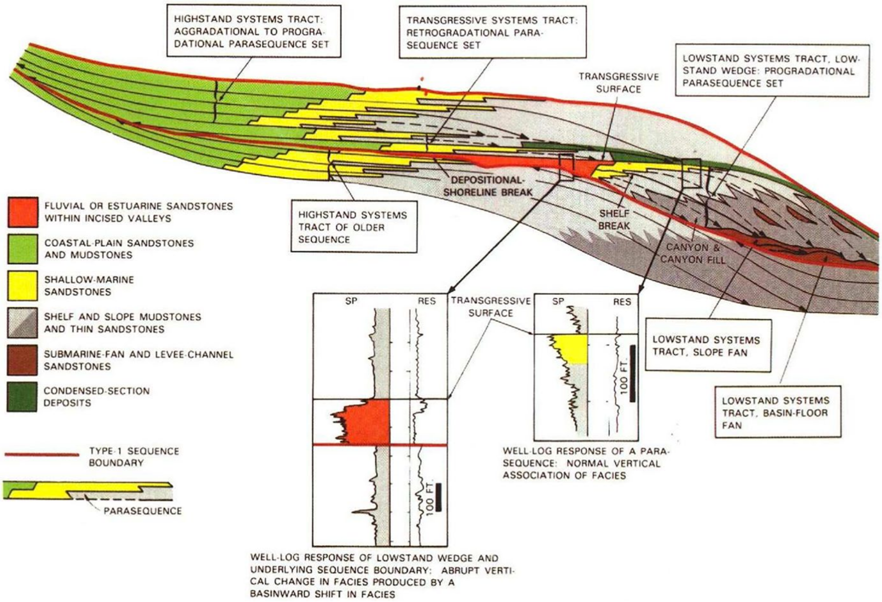

Fig. 4 The basic anatomy of a depositional sequence, comprising stacks of parasequences organized into discrete sedimentary packages, or systems tracts (Van Wagoner et al. 1988, Text-Fig. 2; by permission of the Society for Sedimentary Geology). Major structural features (like a shelf break) are labeled, and depositional environments are coded by color (with a key in the lower left)

The Stratigraphic Distribution of Fossils

As I observed above, paleontologists have long been exercised by worries about the quality of their data. In the 1970s, this led to efforts to construct increasingly comprehensive databases that could, "in idealized form, claim to represent the complete fossil record" (Sepkoski 2013, p. 402). It is hard to overstate the importance of these databases for the history of the field. Research on large datasets illuminated topics ranging from diversification and extinction to guild occupation to changes in ocean biomass over time (Raup and Sepkoski 1982; Sepkoski 1984; Benton 1985; Bambach 1993). However, for studies at the scale of outcrops to sedimentary basins, global taxonomic databases were less useful. Here what was needed were better tools for analyzing the stratigraphic distribution of fossils, and for dissecting the incompleteness of the fossil record into component biases.

The chief attraction of the "new" stratigraphy was its promise to provide these tools for a range of stratigraphic settings. But this benefit was not immediately apparent, and in the years following the publication of AAPG Memoir 26 (1977) the approach made only limited inroads into paleontology. Sequence analysis was first applied to the study of sea-level change during the 1970s, where information from fossils was needed to recognize and interpret sequence patterns and sedimentation dynamics (Hallam 1978, 1988). Later, sequence concepts played a role in the construction of integrated models of depositional environments and paleoecology, like Susan Kidwell's (1954–) influential models of shell accumulation and feedback (Kidwell and Jablonski 1983; Kidwell 1986, 1989). Carlton Brett and colleagues applied sequence stratigraphy to the Devonian rocks of New York state beginning in the 1980s, culminating in the characterization of *coordinated stasis*: a phenomenon in which groups of lineages display concurrent stability over extended periods of time separated by episodes of abrupt change (Brett and Baird 1992; Brett et al. 1996). Prior to the 1990s, however, explicitly paleobiological applications of sequence stratigraphy remained a rarity.

This began to change during the 1990s. Around this time, self-identified paleobiologists were increasingly turning from the museum stacks to the outcrop—to studies that required the collection of fossils in well-resolved spatial and temporal frameworks (Droser 1995; Brett 1998).[24] From these studies, "a new category of research [question]" began to emerge "between the 'traditional' avenues of paleobiology and field-based paleontology" (Droser 1995, p. 507). These questions included:

> Does this turnover correspond with a significant relative sea-level change? ...Do these clades actually radiate in concert? 'Was this extinction gradual or sudden?' Does a basinal pattern reflect taphonomic biases? Can taphonomic biases be corrected for? [and] Can we test patterns of radiations through examination of proxies? (Droser 1995, pp. 507–508)

Droser was careful to note that these questions are not the province of any single methodological approach; yet she also observed that "the integration of stratigraphy with paleobiology is one of the major breakthroughs in the analysis of the fossil record" (Droser 1995, p. 508). Of particular importance was the integration of event and sequence stratigraphy with paleobiology, which had begun to yield insights into biotic responses to climate and sea-level change on local to regional scales (Kauffman 1984; Kauffman and Sageman 1992; Brett and Baird 1996).

But that is not all. In addition to providing high-resolution frameworks for the interpretation of paleontological events, the "new" stratigraphy was also relevant for dealing with biases in the record. These had come under increased scrutiny since the 1960s, as research in taphonomy had expanded from an initial emphasis on fossil preservation to an emphasis on the fidelity of fossil assemblages (Voorhies 1969; Behrensmeyer 1975).[25] However, not all biases affecting the fossil record are the result of selective preservation or postmortem destruction. Others are the result of

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[24] This process received a great impetus from the controversial Alvarez hypothesis, which sparked renewed interest in the phenomenon of mass extinction (Alvarez et al. 1980; see also Sepkoski 2021). Although the most famous early studies of mass extinction were computer-based (e.g., Raup and Sepkoski 1982), other self-identifying paleobiologists studied mass extinction by taking to the field (e.g., Ward 1983).

[25] *Taphonomy* refers broadly to the study of "how organic remains are incorporated into the rock record and the fate of these materials after burial" (Behrensmeyer and Kidwell 1985, p. 105). It has been understudied by historians, but cursory historical treatments can be found in Olsen (1980), Behrensmeyer and Kidwell (1985) and Cadée (1991).

"the selective archiving of the sedimentary deposits that entomb those remains," and these are the subject of stratigraphic inquiry (Kidwell and Holland 2002, p. 562). In particular, they are the subject of sequence stratigraphy, since they concern the distribution of sedimentary environments in the rock record and the processes that structure this record in space and time.

It is considerations of this sort that supplied the focus of Steven Holland's influential modeling study, which appeared in *Paleobiology* in 1995.[26] Bearing the unassuming title, "The stratigraphic distribution of fossils," it was a first-of-its-kind attempt to apply computer simulation to the problem of what controled the distribution of fossils in sedimentary basins. The problem was of wide relevance, since much paleontological research involved the documentation and interpretation of fossil occurrences in basins. Still, Holland's aims in this article were straightforwardly *paleobiological*, as his opening remarks made clear:

> Sequence stratigraphy has revolutionized stratigraphic analysis in much the same way that facies models did decades ago. Many paleobiological and biostratigraphic models require or use stratigraphic testing… Many other paleobiological concepts are based, at least in part, on the distribution of fossils in the stratigraphic record… Therefore, any fundamental change in stratigraphic thought should require a similar reexamination of paleontological thought. (Holland 1995, p. 92)

In pursuing this reexamination, Holland identified three factors that are significant in their effects on fossil distribution and amenable to quantitative modeling. These were: (1) the rarity of fossils (or the chances that a taxon will be represented in a bed where it is expected to occur); (2) facies control (or the probability of collection for a taxon as a function of an environmental variable); and (3) sequence architecture (which controls facies change and sedimentation rates over space and time). Together, these gave an integrated picture of the sedimentary controls on fossil distribution—a picture that both generated predictions about what will be observed in outcrop and suggested sampling strategies for field paleobiological studies.

Holland presented his model in four "steps," beginning with a model of the perfect stratigraphic record and then layering in additional factors to increase realism. In the first, he assumed that any taxon living in a sedimentary basin at a time would be preserved in a bed deposited at that time. So, because the "probability of collection" was 100%, the stratigraphic distribution of fossils would perfectly mirror the true durations of fossil taxa. Step two complicated the picture by simulating collection probabilities of 50%, resulting in a record strewn with gaps, and 10%, resulting in a record that is "more gap than record" (Ager 1973, p. 27). However, because the model lacked any representation of ecology, preserved

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[26] Steven Holland (1962–) is an American paleontologist and stratigrapher, who completed his Ph.D. at the University of Chicago under Susan Kidwell in 1990. I have elected to focus on Holland's 1995 modeling study because it exemplifies the way paleobiologists appropriated resources from the new stratigraphy for distinctively paleobiological ends. But any number of studies from this period might equally have supplied a focus for this section (for example, Kauffman 1984; Kidwell 1986, 1989; MacLeod 1991; Brett and Baird 1992).

fossils were scattered randomly throughout the range of simulated taxa. The third model sought to remove this simplification. It began with the observation that "[m]any, if not most, taxa are most abundant at some particular level of an environmental variable" (Holland 1995, p. 94). In marine environments, the most important variable is water depth; so Holland modeled the probability of collection for nearshore taxa as a function of three parameters: (1) preferred depth, (2) depth tolerance, and (3) peak abundance. Together, these constituted the form of facies control for the model, where *facies control* refers to the influence of water depth on the distribution and abundance of simulated taxa.

Facies control is just one of the complicating factors Holland added to model three. The model also included a representation of water depth change for the simulated section. This was modeled as a series of two shallowing upward cycles bounded by deepening events, matching the pattern of two stacked parasequences. With this factor in the mix, the model generated a number of interesting results. Most notably, the combination of water depth change and facies control produced a characteristic fossil distribution consisting of "a few sporadic occurrences low in the parasequence, followed by a zone in which the fossil achieves a peak abundance, followed by a return to sporadic occurrences" (Holland 1995, p. 96). Parasequence boundaries truncated this pattern when a taxon's preferred environment was close to the boundary—an effect produced entirely by facies change. From this, Holland drew the cautionary message that "[the] abrupt disappearance of a taxon is likely to represent a true extinction where it occurs in the middle of a parasequence, but probably represents facies control when it occurs at a parasequence boundary" (Holland 1995, p. 96).

Yet to confidently interpret ecological and evolutionary processes in sedimentary basins, one had to understand the total effect of stratigraphic architecture on fossil distribution. And for this a complete sequence model was required. Such a model was Holland's fourth model, which consisted of two parts. The first was a model of ecology, in which 1,000 taxa were assigned facies characteristics from a uniform probability distribution. At each time step in the simulation (corresponding to 50,000 years of elapsed time), a taxon had a fixed probability of going extinct. If a taxon went extinct, a new taxon was created for the next time step with randomly generated facies characteristics; so total diversity did not vary over the length of the simulation. This ensured that observed patterns would not be the result of a surplus of originations relative to extinctions for a time interval, or vice versa. Instead, they would result entirely from the filtering effects of sedimentary processes.

The second component of the model was a representation of environmental change and sedimentation. These were simulated using models of basin filling developed for geological applications, in which accommodation is generated through a combination of tectonic subsidence and sea-level change, and sediment is deposited within this envelope according to a diffusion function. Holland's model simulated two depositional sequences, each composed of three systems tracts: the *lowstand systems tract* (LST*), transgressive systems tract* (TST) and *highstand systems tract* (HST) (Fig. 4). The TST consisted of two parasequences; the HST, of six. (No sediment was deposited in the LST.) As in the third model, parasequences were modeled as shallowing upward cycles of deposition bounded at their tops by abrupt deepening events recorded by flooding surfaces.[27]

Each run of the model had three steps. First, a sedimentary basin was generated using a basin simulation. Then, a suite of species was produced, each characterized by a set of randomly generated facies characteristics. Finally, occurrences of each taxon were simulated within the sedimentary basin. For each horizon across the basin, the age and depth of the horizon were used in conjunction with the environmental parameters to determine the probability of collection for a species. This probability was then compared with a random number generator to test for the occurrence of a species at a horizon, and a list of occurrences was compiled. From this a record of first and last appearances was generated, and the number of first and last appearances per section was plotted for each position in the depositional sequence (Fig. 5).

The model produced several results. To begin, it was immediately apparent that the first and last occurrences of fossil taxa were concentrated at particular horizons, not randomly distributed as they would be if the fossil record were unfiltered by stratigraphic architecture. First occurrences were particularly well developed at the four TST flooding surfaces, including the two transgressive surfaces (which mark large changes in water depth). These spikes were dominated by shallow water and environmentally tolerant taxa that originated during the unrecorded lowstand (when no sediment was deposited), or else by deep water and environmentally picky taxa that originated during the LST or the shallow water portion of the previous HST (when preservation of deep water facies was not occurring). Crucially, these spikes did not result from any biological response to sea-level change, since this kind of response was not possible within the model. Instead, they were produced by changing conditions of preservation, and so reflect the way the record was physically assembled.

In a similar vein, last occurrences were concentrated immediately beneath the sequence boundary and the floodings of the TST. The peaks at the sequence

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[27] To understand this section, it is not necessary to understand in detail how sequence stratigraphy narrates the process of sedimentary basin filling. Nevertheless, here is a quick synopsis. At the base of each sequence is a surface known as the sequence boundary. This forms when relative sea-level is falling. During this interval, no new sedimentation occurs, so sequence boundaries correspond to gaps in the rock record. When relative sea-level begins to rise, deposition is renewed and parasequences stack seaward in a net shallowing pattern. These parasequences form the lowstand systems tract (LST), so named because it sits at a topographically lower position than the rest of the sequence. As relative sea-level rise accelerates such that the rate of sea-level rise exceeds the rate of sedimentation, the pattern of stacking is reversed and successive parasequences exhibit a net deepening trend. This set of parasequences comprises the transgressive systems tract (TST). Separating the LST and the TST is a flooding surface called the *transgressive surface*, which marks the point at which seaward stacking is replaced by landward stacking, and is often associated with reduced sedimentation (a phenomenon known as *condensation*). Other flooding surfaces within the TST may also exhibit condensation. Finally, as the rate of sea-level rise begins to slow, parasequences again begin to stack seaward in a net shallowing trend. At this juncture there is another flooding surface, the maximum flooding surface, which records the greatest water depth in the sequence and is often highly condensed. The parasequences deposited atop the maximum flooding surface comprise the highstand systems tract (HST). These are bounded at their top by the sequence boundary, which, again, forms when relative sea-level is falling.

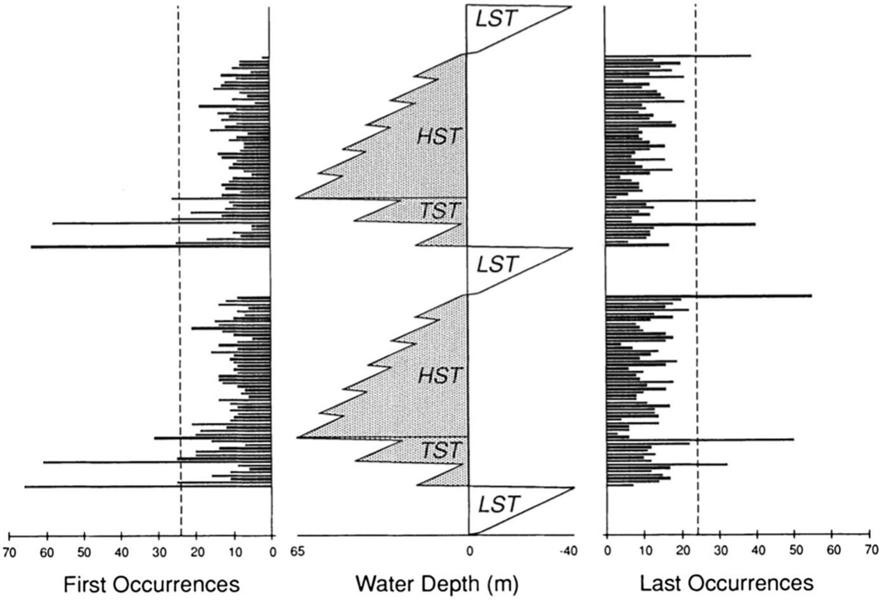

Fig. 5 Results of Holland's complete sequence model, showing numbers of first and last occurrences for single stratigraphic sections throughout two depositional sequences (Holland 1995, Text-Fig. 6; by permission of Cambridge University Press). Time runs along the vertical axis. Systems tracts, corresponding to strata deposited during a phase of relative sea-level change, are indicated in the center of the figure. (Note that no sediment is deposited during the LST.) Major spikes in first occurrences happen just above the sequence boundary (the juncture between the unrecorded LST and the overlying TST) and at all TST flooding surfaces (contacts exhibiting evidence of sharp increases in water depth). Major spikes in last occurrences occur just below the sequence boundary and at all TST flooding surfaces

boundary represented the last occurrence of species that went extinct during the hiatus represented by the boundary. The peaks at the flooding surfaces, by contrast, represented the last occurrence of shallow water species that became extinct after the deepening events recorded by the flooding surface. No spikes in either first or last occurrences were located within the HST, presumably because no major floodings took place during the highstand when sea-levels were falling.

The remainder of Holland's article argued that the simulation of certain taphonomic and ecological gradients modulated but did not change the stratigraphic position of these peaks. This indicated that sequence architecture could predict where the fossil record of sedimentary basins was likely to be particularly misleading—a prerequisite for designing better sampling strategies for fieldworkers. As noted, sequence boundaries were particular hotspots, with clusters of last occurrences expected *beneath* the boundary and clusters of first occurrences expected *above* it. This was an example of an *unconformity effect*, since the major factor generating the bias was unrecorded time. Similarly, last occurrences were expected to cluster beneath transgressive flooding surfaces and first occurrences above them: a symptom of facies control, since it arose from the limited facies tolerance of taxa or the limited availability of certain facies in a succession.

Of course, clusters of first and last appearances in the actual fossil record need not reflect these biases. Some of the most interesting events in life's history involve spikes in origination and extinction rates; one need only think of the mass extinctions that commanded so much attention after 1980 (Sepkoski 2021). However, to recognize these spikes as biologically meaningful, knowledge of sequence stratigraphic architecture is useful, and in some cases, necessary. Here is the ultimate utility of sequence stratigraphic models: that they "reveal not only ways in which the fossil record may be shaped by processes of sediment deposition, but also clues to recognizing those effects and strategies for overcoming them" (Patzkowsky and Holland 2012, p. 111).

There was more to the integration of paleobiology and stratigraphy than models like Holland's. Still, these models provide a good example of how paleobiologists adapted stratigraphic resources for their own, local purposes, fashioning them into tools for paleobiological research at the scale of outcrops to sedimentary basins. In addition, they exemplify an approach to stratigraphic complexity that avoids Darwinian pessimism, on the one hand, and the dangers of more literal approaches, on the other. The approach is basically field paleobiological. Stratigraphic paleobiologists may use computer models like practitioners of generalized rereading, but the purpose of these models is to inform data collection and sampling strategies, as well as to shape interpretations of field data (Holland 2000). Because of this, stratigraphic paleobiology has both participated in, and helped to consolidate, a rehabilitation of fieldwork in paleobiological inquiry. It is the relationship of paleobiologists to "the field," and its implications for paleobiology's disciplinary self-understanding, that I take up in the next section.

Paleobiology, Prestige, and "the Field"

From its consolidation in the 1970s, the science of paleobiology has had an ambiguous relationship with "the field." All paleontology is ultimately based on fieldwork, but this does not mean that every paleontologist—or even every group of paleontologists—is actively involved in producing new collections. A major accomplishment of the paleobiological revolution was to show how much damage a paleontologist could do with only a desktop computer and a library card. Half-seriously, it was said of Jack Sepkoski that his field site was the library; but this was no reprimand spoken under the breath of dusty fieldworkers. On the contrary, it was a fair description of a mode of practice that had taken paleontology by storm, and that came to be identified with paleobiology in particular (Sepkoski 1993). This suggests that to understand the development of paleobiology, some reflection on its relationship to "the field" is necessary.

In *Landscapes and Labscapes* (2002), Robert Kohler characterized the border zone between laboratory and field biology as a lively and contested space structured by an overarching normative regime. Within this regime, labs are special places precisely because they are place-*less*; they are generic places whose seeming universality provides “[a] symbolic guarantee that the science done there is everyone’s, not just someone’s in particular” (Kohler 2002, p. 7). “The field” inverts this logic. Natural spaces are irredeemably particular and variable. That is what makes them interesting epistemic objects. But it also creates problems for fieldworkers, who must contend with the notion that the knowledge they produce is less scientific than the knowledge produced in labs. The trope of the field scientist as a stamp collector underscores the greater value that a culture dominated by laboratories attaches to the universal over the particular (Johnson 2007). In such a culture, any system that escapes the undertow of particularity is likely to be highly valued; lab work is just the most obvious example. It is not the only example, however, and in recent decades, another placeless place has become similarly important. This is the inside of a digital computer, which promises not a view from nowhere, but rather a view from *everywhere*, capable of synthesizing local observations into a consistent and fully synoptic picture of the world (Edwards 2010).

Kohler’s framework provides a useful way of analyzing the history of paleobiology. During the 1970s, a small group of paleontologists sought to “[reinvent] their discipline by creating a new identity for themselves” (Sepkoski 2012, p. 3). The identity was that of a modern evolutionary scientist, but no less important, it was that of a *non*-field geologist. Prior to that time, invertebrate paleontology had been “an almost exclusively field-oriented science” with biostratigraphy and paleoenvironmental analysis as its major applications (Sepkoski 2012, p. 389). As Peter Ward (1949–) recalled of the early 1970s: “a hopeful new paleontologist, arriving in some professor’s office, would be sent away with some assigned geological quadrangle to map, or some quarry to excavate in the hopes of finding one more new species” (Ward 1994, p. 114). This was honest work, but as Gould grumbled in 1980, it did not infuse the profession “with the excitement of ideas” (Gould 1980, p. 98). It also did few favors for paleontology’s reputation, which on the eve of the paleobiological revolution was in a sorry state.[28] In short, paleontology in the early 1970s was in dire need of a makeover, and the early paleobiologists knew how to make it over: by shedding their association with field geology and using the power of digital computers to range god-like over the entire history of life.

This “view from everywhere” played the same role in paleobiology that the fiction of placelessness plays in the lab sciences. Whereas the field is a place of particulars, large databases abstract from these idiosyncrasies to render the fossil record in a completely general way. That is the idea, anyway. As it happened, difficulties kept popping up that limited the power of the approach. For example, early databases, like those compiled by Jack Sepkoski, tabulated only the first and last occurrences of taxa, with no data on geographical range, taxonomic richness, or paleoecology. The result was a powerful tool for generating synoptic pictures of diversity through time, but one that was unsuited for answering questions that involved those unrecorded particulars. Later databases included a richer set of metadata, but the

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[28] Witness the gibe in a 1969 issue of *Nature* that “Scientists in general might be excused for thinking that… most paleontologists have staked out a square mile for their life’s work” (Anonymous 1969, p. 903).

problem remained that computerized paleobiology was less a matter of analyzing particular details than it was of getting away from them.[29] It was a model of practice that traded local detail for the potentially unlimited scope and generalizing power of the view from everywhere.

It is against this backdrop that the integration of paleobiology and stratigraphy is best understood. Field-based or "stratigraphic" paleobiology did not just represent the extension of paleobiology's model-driven approach to problems arising from field data. In addition, it represented an openness to inputs from stratigraphic geology that cut against the rhetoric, and much of the practice, of early paleobiology. One dimension of this openness was intellectual and involved the uptake of new ideas about the structure of the stratigraphic record in space and time. But no less important was a practical dimension, which involved a willingness on the part of paleobiologists to undertake painstaking work to better characterize the field context of fossil collections. Steven Holland did not just build the first integrated model of sequence stratigraphy and paleoecology (an expression of the first dimension of openness). He also established the standard sequence stratigraphic framework for Middle and Upper Ordovician strata in the eastern United States. For this, he was awarded the 2000 James Lee Wilson Award from the Society for Sedimentary Geology (SEPM): a strange honor for a paleo-*biologist*, one might think, but only on the assumption that one must be either a stratigrapher or a paleobiologist.[30]

This two-fold openness has been stratigraphic paleobiology's distinctive contribution to the expansion of the discipline. It consists in a synergy between the two dimensions of openness, in which ideas from stratigraphy inform modeling work, which in turn informs strategies of data collection and analysis. On the data side, sequence analysis facilitates the collection of data in a time-environment framework (Patzkowsky and Holland 2012); and this enables researchers to assess the degree to which a continuous fossil record can be obtained for an environment like the shallow marine shelf. But time-environment sampling also informs the interpretation of documented patterns. Interpreted literally, a pattern may suggest that a taxon disappeared abruptly at a particular juncture in a depositional sequence. However, if that taxon has a strong facies preference, and if the relevant facies is not preserved in the beds surrounding the juncture, the pattern may be an artifact. In particular, if the juncture is a sequence boundary or flooding surface, sequence stratigraphy cautions against a literal interpretation of the data (Holland 1995). This is neither literal rereading nor generalized rereading—it is something else, which leverages interpretive models of the stratigraphic record to tame the complexity of the field without abstracting it away.

Near the beginning of this paper, I observed that the history of paleontology involves significant ruptures imposed upon no less significant continuities. This is true of stratigraphic paleobiology as well. Many continuities link stratigraphic paleobiology to the older tradition of field paleontology, to say nothing of taphonomy,

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[29] Rudwick made a similar observation in his (2018), especially pp. 504–507.

[30] The acronym SEPM refers to the original name of the Society for Sedimentary Geology: the Society of Economic Paleontologists and Mineralogists.

paleoecology, and evolutionary paleobiology. I have focused on Holland's work as an example of how resources from the "new" stratigraphy were appropriated by paleobiologists for distinctively paleobiological ends. But as Mary Droser observed, "[the] wedding of [new] stratigraphic approaches with… paleontology" was already underway when Holland published his model in 1995 (Droser 1995, p. 508). Back in the 1980s, attempts had been made to apply high-resolution event stratigraphy to sedimentary basins, including the Western Interior Basin of North America. This was based on the recognition, inspired by Ager, "that short-term deposits may in fact dominate the stratigraphic record" (Kauffman 1988, p. 606). Using event-beds, paleontologists like Erle Kauffman (1933–2016) were able to construct frameworks for paleobiological inquiry whose resolution often exceeded those of the most exact biostratigraphy (Kauffman 1984). And this is just one example of integration. Susan Kidwell's previously mentioned research on shell accumulation is another (Kidwell and Jablonski 1983; Kidwell 1986). So is David Jablonski's (1953–) work on the biotic effects of marine transgressions and regressions (Jablonski 1980).

All this might seem to nullify my claim that the emergence of paleobiology involved a parting of the ways with stratigraphy. Certainly it would be wrong to say that paleobiologists somehow rejected stratigraphy, for the obvious reason that stratigraphic frameworks supply an important bit of context for interpreting fossil data.[31] Even generalized rereading used data on the stratigraphic range of fossils to formulate its statistical generalizations, so there was never any question of a complete alienation between paleobiology and stratigraphy. Still, the leaders of the paleobiological revolution *did* reject what they perceived to be a subordination of their field to stratigraphy, and this involved denying that stratigraphy had much to contribute to paleontology apart from basic timescales. For paleontology to thrive, practitioners had to cultivate a biological attitude (Rudwick 1968; Gould 1980). But this was unlikely to be advanced by attending to ongoing discussions in stratigraphy, which, anyway, had failed to infuse paleontology with "the excitement of ideas."[32] So, while paleobiologists remained operationally dependent on stratigraphy for bookkeeping, there was little reason for them to engage with it deeply, and still less to establish with it an active "trading zone."[33]

It is true that this adversarial attitude involved a degree of rhetorical posturing. Still, as David Sepkoski has argued, the dominant note in early paleobiological work was conspicuously *non*-stratigraphic (Sepkoski 2012, pp. 389–390). Droser has

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[31] Here it is worth noting that all major figures in 1970s-era paleobiology were trained in traditional paleontological methods. Even Jack Sepkoski, the archetype of the "new model paleontologist," wrote a dissertation titled, "Stratigraphy and Paleoecology of Dresbachian (Upper Cambrian) Formations in Montana, Wyoming, and South Dakota"—hardly the quantitative work he later became known for (Sepkoski 2005).

[32] This traded on the perception that stratigraphy had become bogged down in minutiae (see "Stratigraphy After 1970"), or as the outspoken stratigrapher P.D. Krynine (1902–1964) is reported to have said, that stratigraphy had seen a "complete triumph of terminology over facts and common sense" (Folk and Ferm 1966, p. 853).

[33] By "trading zone," I mean a site of substantive and reciprocal communication characterized by an exchange of materials and ideas. For a more explicit treatment, see Collins et al. (2007).

made a similar point, noting that "most advances in paleobiology specifically have *not* been field based" (Droser 1995, p. 507, emphasis added). Exceptions like Kidwell merely illustrate the point that most paleobiologists prior to the 1990s paid little attention to the "new" stratigraphy. This is what makes the later integration of these fields noteworthy. By cultivating expertise in new stratigraphic methods, a subset of paleobiologists challenged the vision of paleobiology that had been constructed during the paleobiological revolution. A result of the development was to render the distinction between the "old" and the "new" paleontology more ambiguous than it had previously been made to seem. No longer a revolutionary upstart, paleobiology was broadening into a science whose diversity overspilled all attempts to contain it within pre-established disciplinary boundaries.

This final point suggests a reason why historical studies of paleobiology have tended to focus on the events of the 1970s and 1980s. After the 1980s, it is significantly more difficult to identify any well-behaved entity answering to the name "paleobiology." Paleobiology continued to exist, of course, including the institutional entities and practices associated with the paleobiological revolution. But increasingly, the label began to attach to a diffuse and pervasively interdisciplinary research program with strong ties to stratigraphy, geochemistry, systematics, and developmental biology, to name just a few areas. Here the history of paleobiology becomes entangled with that of perhaps a dozen other disciplines, including new hybrids like "geobiology," in ways that remain to be mapped out.

Conclusion

Pessimism about the quality of the fossil record runs deep in paleontology. As Darwin was keen to emphasize, the fossil record is incomplete: "ridiculously" so, to crib a phrase from Ager. This was not unwelcome news for Darwin, since it provided an explanation of the rarity of those transitional forms that must have existed in droves were his theory of gradual adaptive divergence correct. However, by the middle of the twentieth century, the incompleteness of the fossil record had become, in Eldredge and Gould's words, "a catechism that brooks no analysis" (Eldredge and Gould 1972, p. 90). Moreover, it was a catechism whose repetition did no favors for paleontology's reputation. If the fossil record was evidentially impoverished, then paleontologists could have little to say about the major questions in evolutionary biology. A paleontologist could be a good geologist, perhaps, but they could hardly be a creative contributor to evolutionary theory. So, according to Gould and others, something needed to be done.

The leaders of the paleobiological revolution took several courses of action in response to this situation. One was to treat the fossil record as a reliable source of information about at least certain evolutionary patterns (Sepkoski's literal rereading). So, for example, Gould observed that the fossil record "is a faithful rendering of what [modern speciation] theory predicts, not a pitiful vestige" (Gould 1980, p. 184). Others utilized large datasets to avoid the patchy nature of local records (generalized rereading) or used idealized models to circumvent fossils entirely (idealized rereading). Yet none of these approaches was a universal solvent. Literal rereading simply asserted that the fossil record could be trusted, whereas generalized and idealized rereading worked by retreating to scales of analysis where the problems of the fossil record could be ignored or corrected with models.

This paper has traced the emergence of a novel approach to stratigraphic complexity: one that works by analyzing the structure of the record and using this knowledge to inform sampling and interpretation. A key advantage is its ability to analyze stratigraphic incompleteness in the service of more reliable interpretations of field evidence. However, the approach may yet have another effect, which is to suggest a new framing of long-running discussions of "incompleteness" and "bias." According to stratigraphic paleobiology, two sets of processes are equal partners in the construction of the fossil record. On the one hand are biological processes like speciation, extinction, and community assembly. On the other are stratigraphic processes like sedimentation, erosion, and condensation. The task of paleobiology is to analyze how these processes interact to produce the fossil record; it is not to understand how a "once-bountiful tale" is reduced to "a pitiful vestige" through stratigraphic filtering. By emphasizing the structure of the fossil record as opposed to its deficiencies, stratigraphic paleobiology thus threatens to upset a trope that is even older than Darwin's invocation of it in the *Origin* (Rudwick 2008).

It is too early to know whether talk of the structure of the fossil record will replace talk of incompleteness and bias. However, if it does, it will be for reasons that the leaders of the paleobiological revolution would have appreciated. As Holland (2017, p. 1316) observed, "When [paleontologists]… write yet another paper about bias in the fossil record, that is what our colleagues hear. When they hear this repeatedly, they conclude that the fossil record is not worth bothering with." Gould had much the same worry. In his "Task for paleobiology," he chastised paleontologists for their "brutal pessimism" about the fossil record, not least because it implied a subordinate role for paleontology among the evolutionary sciences (Gould 1995, p. 1). Yet Gould had few arguments for why the fossil record should be trusted, apart from the suggestion that certain patterns in the record seem to match expectations from evolutionary theory. The ability to analyze the complexity of the record places paleobiologists in a stronger position. By disclosing how the record is assembled, it enables them to assess when signals from the record can be trusted and when caution is the appropriate response. This is no skeleton key for the cabinets of deep time, but it does represent a noteworthy addition to the project of rereading the fossil record.

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