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Functional Morphology in Paleobiology: Origins of the Method of 'Paradigms'

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Abstract. From the early nineteenth century, the successful use of fossils in stratigraphy oriented paleontology (and particularly the study of fossil invertebrates) towards geology. The consequent marginalising of biological objectives was countered in the twentieth century by the rise of 'Paläobiologie', first in the German cultural area and only later, as 'paleobiology', in the anglophone world. Several kinds of paleobiological research flourished internationally after the Second World War, among them the novel field of 'paleoecology'. Within this field there were attempts to apply functional morphology to the problematical cases of fossil organisms, for which functions cannot be observed directly. This article describes the origins of the kind of functional inference for fossils that I proposed in 1961 as the method of 'paradigms' (a year before Thomas Kuhn made that word more widely familiar with a quite different meaning). Here I summarize some of my 'worked exemplars', which were intended to show the paradigm method in action. These case-studies were all taken from the paleontologically important phylum of the Brachiopoda, but the method was claimed to have much wider implications for the interpretation of the fossil record in terms of adaptive evolution. This article takes the history of the paradigm method as far as the late 1960s. I hope to trace, in a sequel, its ambivalent fate during the 1970s and beyond, when for example Gould's critique of 'the adaptationist programme' and the rise of computer-based quantitative methods for the evolutionary interpretation of the fossil record led to the relative eclipse of functional morphology in paleontology.

Keywords: Paleobiology, Functional morphology, Paradigm, Brachiopods, Martin Rudwick

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Introduction

This article describes the historical origins of the method of 'paradigms' as a way of analyzing organisms in terms of their functional morphology, when functions cannot be observed directly because the organisms are extinct and only known as fossils. Working in the 1950s within the research tradition of 'paleobiology', I first proposed the paradigm method of functional inference in 1961. Here I summarize my use of it up to the point (in 1971) at which I ceased to contribute directly to paleontological research, having in 1967 moved my professional field of teaching and research into the *history* of paleontology and other natural sciences. This article is partly autobiographical; but I should emphasize at the start that it is not my intention to use it to rehabilitate, vindicate or celebrate my earlier research, but simply to use the evidence of my publications and those of my then collaborators and critics, supplemented by a few unpublished sources and my personal recollections, to reconstruct a significant phase in the twentieth-century history of the science of evolutionary paleontology. I hope in a separate article to continue this narrative by describing the reception of the paradigm method among other paleontologists during the 1970s and 1980s, and to trace its ambivalent fate in paleontological practice, in the face of strong criticism of the concept of pervasive adaptation that it was said to embody. (The background history sketched in the next two sections of this article is necessarily based on the limited secondary literature currently available, supplemented by my own recollections and those of my contemporaries; it may be modified substantially by further historical research on early and mid-twentieth century paleontology, for which there is a great need.)

The Origins of 'Paleobiology'

It is easy to dismiss the way that paleontology was pursued before the late twentieth century as unimaginative and pedestrian, because much of it was devoted to the description, classification and naming of fossils, with little regard for what the organisms might have been like while they were alive. But there was a specific reason for this imbalance, which reaches back to the early history of the science.

Ever since the most creative period in the history of geology, in the late eighteenth and early nineteenth centuries (reviewed in Rudwick, 2005, 2008), the common fossil remains of invertebrate animals have

usually been treated in a different way from the far rarer remains of vertebrates: William Smith has been taken retrospectively as the central figure for the first kind of study, Georges Cuvier for the second. Smith's concept of 'characteristic' fossils made the often abundant fossil remains of invertebrates, such as mollusc shells, an invaluable tool for working out the structural sequence of rock formations in 'stratigraphy' (Smith's own new word for it). The rich 'fossil record' provided by the remains of invertebrates became an essential part of stratigraphical geology, and during the nineteenth century most paleontological research therefore came to be embedded institutionally in the geology departments of universities and in geological surveys. However, the way that rock formations were given relative dates by means of fossils was no different in principle from the way that they could have been dated, supposing—however improbably—that distinctive kinds of micro-meteorites had been found to be similarly 'characteristic' of specific rock formations and hence of successive periods of cosmic and terrestrial history. That fossils were of organic origin was strictly irrelevant to their practical use in Smithian stratigraphy. In effect, the *instrumental* role assigned to the vast bulk of fossil material led to the institutional separation of most of paleontology from the biological sciences, and hence to the marginalising of any fully biological interpretations of invertebrate fossils.

In contrast, Cuvier's concept of the integration of function with structure in vertebrate animals became his invaluable key for reconstructing extinct species of mammals and reptiles from their usually scattered bones, and for bringing them back to life at least in the mind's eye; and this later facilitated the reconstruction of their likely phylogenies or evolutionary histories. The fossil record of vertebrates therefore became an important part of evolutionary biology, and during the nineteenth century research on them came to be embedded mainly in the biological departments of universities and in museums of natural history. (Fossil plants, and the '*paleobotany*' based on them, do not fit readily into this oversimplified scheme, but will not affect my argument.)

The science of fossils was first given the name '*paléontologie*', broadened from an initial suggestion of '*paléozoologie*', in the early nineteenth century (Rudwick, 2008, pp. 47–48). Not surprisingly, the word was proposed in French, the then international scientific language, and by a naturalist in France, the world's then leading scientific nation. It served well for the following hundred years, while the science expanded vastly in scope. In the course of the nineteenth century, paleontology became essential both as a tool for stratigraphical geology and

as primary evidence for reconstructing the large-scale history of life and later explaining it causally in terms of evolutionary processes (Darwin's theory of very slow 'descent with modification' by means of 'natural selection' being just one of many such candidate explanations). In the first of these roles for paleontology, the biological character of the organisms that had left fossil remains was, as just noted, strictly irrelevant. But also in the second, more surprisingly, the use of fossil evidence to reconstruct phylogenies, with an emphasis on preserved and observable *structures* and their inferred transformations through time, led paradoxically to the relative neglect of reconstructions of the changing *functions* and ways of life that the evolving structures or anatomies might have served or made possible. The biological science of '*morphology*', which flourished throughout the nineteenth century, became focussed predominantly on the topological transformations of anatomy—within an evolutionary framework of one kind or another—rather than on the adaptive significance of anatomy in '*functional morphology*' (the classic account of these debates is in Russell, 1916). The rejuvenation of evolutionary theorising in the 'Neo-Darwinism' of the early twentieth century, although highly productive in other ways and despite its accent on natural selection, did little to revive in paleontology the pre-Darwinian interest in functional morphology.

This weakness in paleontology was recognised explicitly in the early twentieth century in German-speaking central Europe, which by then had overtaken France to become the world's leading scientific region. The Austrian palaeontologist Othenio Abel (1875–1946) proposed the new word '*Paläobiologie*'—superficially a synonym of '*Paläontologie*'—to denote 'the investigation of the adaptations of fossil organisms and the determination of their ways of life [*Lebensweise*]'. This was in his *Grundzüge der Paläobiologie der Wirbelthiere* (Abel, 1912)—titled on its cover just *Paläobiologie*—which applied the concepts of functional morphology to fossil vertebrates. His *Paläobiologie der Cephalopoden* (Abel, 1916) then took fossil cephalopod molluscs and their living relatives as an example of what could be done with invertebrates; later, after the Great War, his *Paläobiologie und Stammesgeschichte* (Abel, 1929) related it to his evolutionary ideas. By that time his chair at the University of Vienna had been redefined to include *Paläobiologie*. Abel also founded and edited (from 1928) the mainly German-language journal *Palaeobiologica*, subtitled an 'Archive for the investigation of the life of the past and its history', which published important primary research in this area. Abel himself was just the most prominent figure in a broad movement

among paleontologists in continental Europe during the interwar period, which developed the idea of 'paleobiology' as a distinctive kind of paleontology, much more closely related to other biological sciences than to geology. [Abel's involvement with the politics of National Socialism in the 1930s (Rieppel, 2012) may have contributed to the marginalising or neglect of his concept of paleobiology, outside Germany, after the Second World War.]

In contrast to continental Europe, the bulk of paleontological research in Britain continued in the interwar and postwar periods along traditionally stratigraphical and taxonomic lines, for example in the papers read (rather infrequently) at the Geological Society in London and in the substantial monographs published by the Palaeontographical Society. Paleontologists were trained in British universities primarily in geology departments, and many of them found employment in geological surveys at home or abroad. With a few important exceptions, British paleontologists did not have close scientific relationships with their colleagues working in biological departments. Even when, eventually, they began to assert their independence from geology, their science remained in practice quite conventional. In 1957 some of them founded a new Palaeontological Association, having despaired of gaining an adequate voice within what they regarded as a moribund Geological Society. They gave its new journal the plain title *Palaeontology*, and made a point of offering its authors a generous allowance of high-quality collotype plates and other illustrations. But although this helped to improve the science's internal standards, most of the papers published there continued for many years to be primarily descriptive and taxonomic in character and stratigraphical in orientation.

The emergence in Britain of more biologically oriented research on fossils was most noticeable in the Department of Geology in Cambridge. Here there was a greater emphasis on paleontology than in any other British university. The department was housed (as its enlarged successor 'Earth Sciences' still is) in a building dominated by the Sedgwick Museum, a huge collection of fossils from around the world, the core of which had been assembled by the great nineteenth-century Cambridge geologist Adam Sedgwick. The collection was arranged conventionally, that is stratigraphically, from Cambrian to Pleistocene: in material form it displayed almost the entire known fossil record. Its one notable limitation was that, although a few spectacular skeletons of large fossil vertebrates had long been on show, its collections were in practice used mainly for teaching and research on invertebrates. Vertebrate fossils were studied on the opposite side of the same street, in the

university's Department of Zoology; this was a dichotomy that struck younger Cambridge paleontologists at this time as both regrettable and artificial. Apart from that limitation, paleontology in mid-century Cambridge's geology department was unusually paleobiological in character. Whereas the introductory teaching treated fossils in a traditional Smithian manner that many students found stultifying—having to recognize and name dozens of British 'characteristic fossils' and to learn their stratigraphical ranges—the advanced lectures in paleontology were organized biologically, by phylum rather than stratigraphically, and in practical classes students were able to handle rare and outstandingly fine specimens from the museum's collections. There was an emphasis on the close study of morphology as the indispensable basis for taxonomy and phylogeny as well as being essential for any true 'paleobiology' (Hallam, 2009, pp. 423–424).

This was due at least in part to the presence of Oliver Bulman (1902–1974), who in 1934 had been appointed 'Lecturer in *Palaeozoology*', a designation—very rare at that time in the anglophone world—that he retained when in 1945 he was promoted to Reader (Stubblefield, 1975). Bulman was an expert on graptolites, an abundant but enigmatic and totally extinct group of fossils that was of great practical value in Paleozoic stratigraphy. But his research had become unusually paleobiological (or paleozoological) in character. This was probably a result of his contacts with paleontologists in continental Europe during his travels in the interwar years, when he studied museum collections of the rare and precious cases of exceptionally well preserved graptolites: he contributed the section on graptolites (Bulman, 1938) for the *Handbuch der Paläozoologie* (Schindewolf, 1938) edited by the leading German paleontologist Otto Schindewolf (1896–1971) of Tübingen. Bulman collaborated with his continental colleagues to reconstruct in detail the morphology and mode of growth of these colonial organisms, to infer their modes of life, to piece together the phylogeny of the group, and to clarify its puzzling zoological affinities (traditionally with coelenterates but by this time thought to be with early chordates). After the war, his volume on graptolites (Bulman, 1955) was one of the first to be published in the huge international *Treatise on Invertebrate Paleontology* (Moore, 1955–1971). Bulman's presence in Cambridge, combined with that of several other paleontologists, made its geology department potentially more receptive to newer kinds of research on fossils than any other in Britain. In 1955 he was appointed the head of the department and its one and only Professor, the first time that this influential position had been held by any paleontologist.

In the United States, the situation of paleontology was similar to Britain. The *Journal of Paleontology* was founded in 1927, not by the Paleontological Society but by the Society of Economic Paleontologists and Mineralogists, and primarily for the publication of papers on fossils 'helping the understanding of American stratigraphy', particularly the microfossils (e.g., foraminifera) most useful to the oil industry. In fact the journal's original goals were not intrinsically biological at all: its founding editor stated that papers on 'the use of mineral grains for [stratigraphical] correlation' would also be acceptable (Cushman, 1927). This exemplified the stratigraphical orientation of most of invertebrate paleontology in the United States (Rainger, 2001). In contrast, one of the first American scientists to use the term '*paleobiology*' was George Gaylord Simpson (1902–1984), who was then a young vertebrate pale-ontologist at the American Museum of Natural History in New York, and who was greatly impressed by Abel's work (he was unusual among his scientific compatriots in being able to read German with ease). Simpson described his early monograph on Mesozoic mammals as 'a study in paleobiology', and explained that he was treating them 'not as bits of broken bone but as flesh and blood beings' (Simpson, 1926, p. 228; 1928). In subsequent years he became a leading American exponent of 'paleobiology', though it remained at first an unusual word. How-ever, Simpson later came to identify his approach not so much with the reconstruction of the specific adaptations and ways of life of the extinct organisms themselves—as 'flesh and blood beings'—but rather with the causal explanation of the patterns and processes underlying evolution-ary changes at the species level and above, as expounded in his highly influential *Tempo and Mode in Evolution* (1944) and *The Major Features of Evolution* (1953). In effect, however, this diverted his attention away from questions of functional morphology.

In the postwar period, 'paleobiology' became a controversial term in the United States, for there were forceful arguments between paleon-tologists calling for the independence of their science from the demands of stratigraphical geology, and others who insisted on the maintenance of those links. In 1947, for example, Marvin Weller (1899–1976), one of the latter, stated bluntly that 'Any student of fossils who does not have a strong, abiding and well-founded interest in geology and a thorough training in that science is not a paleontologist. He is simply a paleobi-ologist' (Weller, 1947, p. 572; Sepkoski, 2012, pp. 52–59). One of the most vigorous responses to this came from Simpson's colleague Nor-man Newell (1909–2005), who claimed that the study of fossils—and especially invertebrate fossils—was being stunted by paleontologists'

lack of biological training and their failure to develop an evolutionary perspective. Newell proposed that 'paleobiology'should be treated as a science distinct from 'stratigraphical paleontology'; he argued that the 'restoration of the life of the past' in all its dimensions was distinct from the 'applied paleontology' that used fossils merely as 'a tool' for stratigraphical correlation (Newell and Colbert, 1948, pp. 265–266).

However, the meaning of 'paleobiology' was quite fluid, even among those American palaeontologists who were positive about its use. In 1958, for example, Arthur ('Gus') Cooper (1902–2000), who was in charge of the Department of Geology at the U. S. National Museum in Washington D. C., used his presidential address to the Paleontological Society to express his concern that stratigraphical interests had skewed his science away from its proper focus on 'descriptive, taxonomic, and morphological' research. Like Newell he claimed that 'paleontology is in reality paleobiology, an independent science'. Listing its components, he gave pride of place to 'morphology, the very foundation' of the science; then taxonomy, evolution, and distributions in time and space; then what he noted as the *novel* field of 'paleoecology, a subject that has presently come to the front'; and only in last place stratigraphical correlation (Cooper, 1958, p. 1012). In 1963 Cooper's Department of Geology was split, on his initiative, into 'Paleobiology' and 'Mineral Sciences'. But this simply separated the study of fossils from that of terrestrial objects and materials of inorganic origin; it did not in itself entail any radical change in the way in which fossils were studied at the Museum, which continued to be primarily taxonomic in its objectives.

The Diversity of 'Paleobiological' Research

The prominence of the quantitative, statistical and computer-driven research that was pursued in the 1970s and 1980s by the founders (in 1975) of the journal *Paleobiology*—in the retrospectively defined 'quantitative' or 'paleobiological revolution' (Sepkoski, 2005; Sepkoski and Ruse, 2009)—has tended to overshadow the diversity of the biologically oriented work that flourished increasingly in the paleontology of the previous decades. While traditional paleontology continued to be focussed on the precise description and classification of fossil specimens of all kinds, usually oriented towards stratigraphical objectives, several loosely linked areas of 'paleobiology' emerged in the anglophone world in the 1950s and 1960s. What they had in common was simply the goal of using fossil evidence to understand the long-term *history* of life,

including of course its evolutionary history. This was a dimension that palaeontologists regarded as being almost closed to those biologists ('*neontologists*') who neglected fossil evidence and only studied living organisms (phylogenies based solely on the latter being regarded as highly problematic). Here these areas of paleobiological research must be summarized very briefly.

The group of paleontologists who spearheaded the putative 'revolution' were not the first to try to compile a comprehensive *database* (as its digital successors would now be called) of the fossil record, with the aim of drawing general conclusions about major features of the history of life; its origins reach back into the nineteenth century, for example in the work of Heinrich Bronn (Rudwick, 2008, pp. 166–172). Nor, in the twentieth century, was this effort confined to North America. In Britain the Cambridge geologist Brian Harland (1917–2003), a strong advocate of continental mobilism or 'drift' long before it became fashionable, was also the driving force behind the compilation of *The Fossil Record* (Harland et al., 1967; I was one of the many *alia*), which harnessed the expertise of paleontological specialists around the world to record in stratigraphical terms the *first* and *last* known occurrences of appropriate taxa of fossil organisms. This was explicitly intended to act as an indefinitely improvable collection of data for making broader inferences about the history of life: for example to evaluate ideas about geologically rapid adaptive radiations, and the then highly controversial ideas about possible episodes of rapid mass extinction. The work also included a pioneer attempt to use the power of early computers to analyze quantitatively the results of the compilation. Primarily, however, it was designed simply as a reliable source of objective data about the known stratigraphical ranges of fossil taxa, in contrast to the conjectural ranges often attributed to them in order to support hypothetical reconstructions of their phylogenies. And Harland's earlier compilation of *The Phanerozoic Time-scale* (Harland et al., 1964), which assembled the relevant experts' latest and best radiometric dates, gave the fossil record a quantitative or 'absolute' chronological dimension.

The other areas of paleobiological research that were emerging in the 1950s and 1960s were all primarily qualitative in character, but were not for that reason any less significant. In fact they illustrate how an emphasis on the quantitative element in scientific practice—often with the far from subtle insinuation that the qualitative is inferior—can lead to some questionable historical evaluations of past research.

One of these new or at least enlarged areas of qualitative paleobiological research flourished from the 1950s onwards in the wake of the

discovery of diverse microfossils in Precambrian rocks. This showed that there was a previously unsuspected fossil record reaching far back into the pre-Phanerozoic (Precambrian) history of the Earth, which in the light of early radiometric dating had turned out to be unexpectedly vast in length relative to the whole of Phanerozoic history (Cambrian to present). Such discoveries led to intensive debates, integrating the biological with the physico-chemical, about the evolution of the hydrosphere and atmosphere in relation to the early history of life itself (Cloud, 1988; Schopf, 2009). In much the same years came the recognition of a distinctive assemblage of quite large but wholly 'soft-bodied' organisms, named after the remote Ediacara hills in South Australia but found much more widely (Glaessner, 1958, 1961; Turner and Oldroyd, 2009): these had flourished shortly before the apparent 'Cambrian explosion' of diverse metazoan life (in, of course, geologists' conception of 'shortly' and 'explosion'!). That event in turn was put into perspective by the intensive re-study, from the late 1960s, of the spectacularly varied and well preserved organisms, most of them 'soft-bodied', found in the Burgess Shale high in the Canadian Rockies (Whittington, 1985). This Cambrian formation was the oldest known case of the rare '*Lagerstätten*' that had long given paleontologists a few tantalizing glimpses of the rich diversity of past faunas; they highlighted the limitations of the ordinary fossil record, restricted as it usually is to organisms with easily preserved 'hard parts' such as shells and bones.

The interpretation of such exceptional deposits was beginning to be related to an analysis ('*taphonomy*') of the ways in which, in diverse environmental circumstances, organisms may come to be fossilized in various ways or leave no trace at all. Associated with such studies, closer attention was beginning to be given to the '*trace fossils*' that had long been noticed by paleontologists but often dismissed as almost worthless because the animals themselves were rarely preserved. From the 1950s, however, these traces of animal behavior, such as tracks and burrows, were analyzed systematically (as '*Palichnologie*'), particularly by paleontologists in the German-speaking world; an outstanding young exponent was Adolf Seilacher (1925–2014) of Tübingen, Schindewolf's former student and later his successor (Seilacher, 1953a, b). As in other examples of these newly paleobiological kinds of research, vertebrate paleontologists had a clear head start: studies of the tracks of dinosaurs and their interpretation in terms of anatomy and locomotion had already begun, and fruitfully so, back in the nineteenth century (Rudwick, 2008, pp. 151–153; Cohen, 2011, pp. 30–64).

The interpretation of the trace fossils made by invertebrates, and sometimes identifiably due to specific extinct animals such as trilobites, was just one sign of a much broader movement that, as Cooper noted, was emerging among paleontologists in all the scientific nations in the first postwar decades. This was the idea of '*paleoecology*', the reconstruction of the varied environments in which the organisms of the deep past had flourished, in so far as these habitats could be inferred from the fossils themselves and from the sediments in which they were preserved. Paleoecology had its conceptual roots back in the nineteenth century, with the recognition of the limitations of Smithian stratigraphy: fieldwork showed that sediments of distinct kinds, with equally distinct 'characteristic' fossils, had often accumulated *at the same time* in different areas. These '*facies*' were interpreted as the products of distinct environments: in the example for which the term was first proposed (in the Jurassic formations of the Jura hills on the Franco-Swiss border), these were coral reefs with shallow lagoons on one side and open sea on the other (Rudwick, 2008, pp. 455–460). The recognition of distinct facies was often treated by stratigraphical geologists as an unwelcome complication, a deviation from a straightforwardly sequential 'layer cake' or pile of rock formations. It was therefore a sign of a more paleobiological approach that the new 'paleoecology' developed a systematic analysis of specific assemblages of fossils embedded in particular kinds of rock, which were interpreted as the traces of specific communities of organisms adapted to particular physical environments.

In one of the first comprehensive reviews of this field, the British paleontologist Derek Ager (1923–1993) began his *Principles of Paleoecology* with a ringing declaration that 'If paleontology is to progress beyond stamp-collecting [the stereotypical physicists' dismissal of sciences less quantitative than their own], we must consider fossils as living organisms' (Ager, 1963, p. vii). That such a sentiment was still thought necessary, even in the early 1960s, says much about the continuing dominance of stratigraphical paleontology and the relative novelty of any paleobiological approach. Ager divided his subject into two parts, adapting terms already current in studies of living organisms. The analysis of communities of organisms and their collective adaptations to their environments was '*paleosynecology*'; the analysis of individual organisms and their individual adaptations and ways of life was '*paleoautecology*'. The latter was in fact a new name for studies that already had their own long pedigree. Fossil vertebrates, and at least a few invertebrates, had been analyzed in this way, ever since Cuvier for example interpreted a then unique specimen of a '*ptéro-dactyle*' (in

modern terms a Jurassic pterosaur) as a *flying reptile* without parallel in the present world (Rudwick, 2005, pp. 499–502). That tradition had flourished subsequently, through the rest of the nineteenth century, with the well known reconstructions of mammoths, dinosaurs and other popular fossil wildlife, depicted or displayed in their reconstructed environments (Rudwick, 1992); and it had continued in the twentieth century in the *Paläobiologie* of Abel and many others.

The same kind of analysis of *structure* (or morphology) in terms of *function* (or adaptation) was of course a well established method in the study of living organisms, and not only vertebrates. But the application of functional morphology to *fossil* invertebrates was considered highly problematic, unless their morphology was close to that of related living invertebrates whose functions could be directly observed and even subjected to experiment. Where that condition was fulfilled, important work could be done. An outstanding example was the interpretation, by the young British zoologist David Nichols (1930–), of the micro-evolution of the Cretaceous sea-urchin *Micraster* in terms of changing adaptations and modes of life (Nichols, 1959a, b). This very rare case of continuous morphological changes that could be traced through an exceptionally unbroken and uniform sequence of strata (in the Chalk formation of southern England) had been well known since the turn of the century; and in the postwar period it was re-studied with modern biometric and statistical methods (Kermack, 1954). But its detailed interpretation as a story of continuous *functional* or adaptational change (from a shallow to a deeper burrowing infaunal habit), was strikingly novel. As a zoologist, however, Nichols made it clear that this was crucially dependent on biological knowledge of the functional morphology of living echinoids.

In contrast, many palaeontologists regarded functional interpretations with suspicion or scepticism, and as little better than speculations: one paleontologist's guess, it was often said or at least implied, was as good (or otherwise) as that of any other. This attitude effectively discouraged or even inhibited research on the functional morphology of fossil invertebrates.

The Making of a Paleobiologist

At this point it is useful to focus on the experience of one paleontologist who was active in the 1960s, namely myself (Martin Rudwick, 1932–). This will indicate what was specific to my intellectual trajectory, against

the background of what, as just summarized, was characteristic of the time. Like many other paleontologists, it was a childhood fascination with collecting fossils that first led me to a serious study of the rocks in which they were found and hence to the science of geology. As a Cambridge undergraduate (from 1950), the university's Department of Geology became my institutional base; this, as already noted, was an exceptionally favorable environment for an aspiring paleontologist in Britain. But I also crossed the street to study zoology as a separate subject. A specifically paleobiological interest—uniting the two sciences—first became apparent when I used a lecture to the Sedgwick Club, the student geological society, to talk about paleoecology; this, as just noted, was at the time a quite new and unfamiliar area of research.

Not surprisingly my own research began, after graduation in 1953, as an attempt to interpret a sample of stratigraphy in terms of the paleoecology of its fossils. Under the guidance of Joscelyn Arkell (1904–1958), at this time the world's leading expert on Jurassic stratigraphy and ammonite taxonomy, I studied some of the English Jurassic formations, which had been well explored since the nineteenth century. I planned to re-interpret some of the complex sequences of strata and their fossils in terms of equally complex sequences of environments (this was 'paleosynecology'). However, most of the rock exposures, apart from coastal cliffs, had become so overgrown and the stratigraphy therefore so obscure that the project soon came to seem unpromising. On the other hand, finding the fossils and then studying them closely back in Cambridge focused my attention on their morphological features, raising questions about their modes of growth and the functions that they might have had in life (this was 'paleoautecology'). Two classic books, which my biology teacher at school had first urged me to read, came to seem intriguingly relevant: they were D'Arcy Thompson's *On Growth and Form* (1917/1942) and E. S. Russell's *Form and Function* (1916). In effect, these works introduced me to the *morphological* tradition, which had flourished in the biology of the nineteenth century and early twentieth, before being marginalized by the rise to dominance of the 'Modern Synthesis' of Neo-Darwinian evolutionary theory. My research now became strongly morphological and paleobiological in orientation, aspiring to be a study of 'growth-and-form-and-function' in fossils. In view of the general scepticism of paleontologists about the value of functional morphology in their science, this was a decidedly bold—or rash—research topic for a beginner to choose. But Bulman, who with Arkell's approval became my new 'research supervisor', encouraged this change of direction.

I focused my work on one specific group of invertebrate animals, which were abundant and attractive fossils in the Jurassic strata where my research had begun. However, those of any and every stratigraphical level and geological age were now potentially relevant, and the rich resources of the Sedgwick Museum were therefore invaluable. My chosen group—in zoological terms a distinct phylum—was that of the *brachiopods*. These animals were often relegated by zoologists to the status of a mere 'minor phylum', since few kinds are still alive in the seas of the present world. But to paleontologists the brachiopods were a major phylum, with a rich and exceptionally continuous fossil record from the Cambrian period onwards. My long-term research plan was therefore to try to interpret the morphological features of fossil brachiopods of any and every geological period in terms of their likely functions and adaptations, and hence ultimately to interpret the large-scale phylogeny of brachiopods in terms of the evolutionary history of the animals' modes of life. I hoped this might throw light on major features of evolutionary biology such as adaptive radiations, convergence and parallel evolution, and what looked suspiciously like episodes of mass extinction.

All this was clearly paleobiology, as that term was later understood in the anglophone world; but like some of my contemporaries I was aware of the precedent already set by *Palaeobiologica* in the interwar German-speaking world and, closer at hand, by Bulman's designation of himself as a 'palaeozoologist'. When in 1956 I entered Trinity College's competition for junior research fellowships, I defined the area of my proposed dissertation not as paleontology but as '*palaeozoology*'. Specifically, it was on 'The Functional Morphology of Fossil Brachiopods' (Rudwick, 1956), which highlighted the biological concept that I hoped to apply systematically to this paleontologically important phylum. In the dissertation's non-technical summary—which was required to be intelligible to an electoral committee that might range from classicists to mathematicians—I introduced it with a sketch of the *history* of paleontology (here I unknowingly anticipated my much later career as a historian of the sciences). I argued that while the functional interpretation of fossil organisms had been prominent in the early years of paleontology (as in Cuvier's work), it had later been eclipsed, paradoxically, by the rise of evolutionary ideas (in the wake of Darwin's *Origin*), which had diverted attention away from reconstructing vanished ways of life into reconstructing phylogenetic pathways: 'It is as though a monograph on fine china were to trace the cultural and artistic influences underlying the design of a Wedgwood tea-pot without men-

tioning the suitability of the object for pouring tea'. I claimed that the pre-Darwinian emphasis on functional morphology in paleontology needed to be revived and then integrated with the modern world of evolutionary theory; 'the resultant synthesis', I concluded, 'may prove a useful contribution to biological science as a whole'.

The Making of the Paradigm Method

In the same dissertation summary, I explained that 'The chief aim of this work, at this early stage, has been the formulation of a method, rather than the achievement of extensive results'. The method was what I later called the method of '*paradigms*'. Although I did not use this then unusual word in print until 1961—just one year before Thomas Kuhn's *Structure of Scientific Revolutions* (1962) made it much more widely familiar with a quite different meaning—the concept behind it was already clear in an extended methodological section of my 1956 dissertation (which was revised for my PhD in 1958). In the dissertation's non-technical summary I illustrated it by extending my 'ceramic analogy':

> Someone unfamiliar with tea-drinking might be able to deduce the function of the spout of a tea-pot from its structure and design, but only after making the assumptions that the spout was not purely ornamental, and that it was so designed that it could fulfil its function with efficiency…. A study of the spout in the light of hydrodynamical principles would show that its form was well adapted to the outward flow of a not-too-viscous fluid and the formation of a smooth and even jet when the pot was tilted.

I argued that if in reality the spout had been used not for pouring tea but, say, to house the wick of a 'Grecian lamp'—an object rather similar in form to a tea-pot—its structure would have been demonstrably inefficient on several counts. Alternative functional interpretations could thus be *tested* for their relative plausibility. If some other feature of the tea-pot proved intractable to any such functional analysis, 'it would be necessary to conclude either that its function was beyond deduction from the evidence available, or that it had had no function': for example, the Neoclassical decoration on the tea-pot would be recalcitrant, because its function was not physical but aesthetic and socio-cultural. Thus the proposed method did not entail any assumption that *all* features of the tea-pot—or of a fossil organism—must have had

functional or adaptive value in physical terms, still less that they all operated with perfect efficiency; only that some functional interpretations might have demonstrably greater likelihood than others of being on the right lines, and that the alternatives could be tested and evaluated in the light of appropriate physical or mechanical principles, and hence in some cases by appropriate experiments.

As a way of explaining this proposed method of functional inference, my 'ceramic analogy' of a tea-pot was not chosen arbitrarily: in the case of these fossil organisms some of the relevant physical principles were indeed those of hydrodynamics. Almost all brachiopods, living and extinct, have or had two shelly '*valves*' tightly hinged together, with matching margins tightly juxtaposed so that when the shell is closed the interior is or was tightly insulated from predators or other external dangers. (Brachiopod shells are bilaterally symmetrical, but with the valves dorsal and ventral, unlike the left and right valves of bivalve molluscs such as mussels and clams.) When the shell is opened and the valves gape apart, all living brachiopods pump slow but steady currents of sea water in and out of a large '*mantle cavity*' inside the shell. Within this space a complex organ, the '*lophophore*' (analogous to the gills of bivalve molluscs), bears specialised cilia that severally and simultaneously create the currents, catch suspended food particles out of the water, and convey them entangled in mucus to the animal's mouth at the back of the mantle cavity. This '*suspension-feeding*' (or 'filter-feeding') system of water currents, which is closely matched in many unrelated animals such as bivalve molluscs and ascidians, is essential to the way of life of living brachiopods. If it was also used by extinct forms it would necessarily have had to operate according to the same hydrodynamical principles.

After I was awarded a research fellowship at Trinity College, the customary sociability of its 'High Table' enabled me to talk informally about this research—right across the university's often rigid departmental frontiers—with some much more senior scientists. Among them was the distinguished fluid dynamicist Sir George ('G. I.') Taylor (1886–1975), with whom I was able to discuss the hydrodynamical issues involved in reconstructing the likely suspension-feeding systems of extinct brachiopods, and who patiently explained to his junior colleague, without daunting mathematics, the important distinction between laminar and turbulent flow, the significance of Reynolds numbers, and much else that was relevant.

Matching Taylor's hydrodynamical input into my emergent paleobiology was the influence of Carl Pantin (1899–1967), the equally dis-

tinguished professor of zoology in the university, whose own research was focussed on the operation of the nervous system in coelenterates and other invertebrates (Russell, 1968). In my dissertation I had made crucially important use of Pantin's influential presidential address to the zoology section of the 1951 meeting of the British Association. Pantin's 'Organic design' (1951) had been taken as giving biologists license, as it were, to use 'design' language in describing organisms and analyzing their functional morphology, without being suspected of importing the questionable deistic metaphysics of William Paley's classic 'argument from design'. Citing D'Arcy Thompson's 'magnificent' *Growth and Form*, Pantin had adopted the design of bridges as an extended analogue; and he had used copious biological examples to argue that convergence and parallel evolution, far from being occasional and curious anomalies, were bound to be common and indeed pervasive:

> In this universe of ours any functional problem must be met by one or other of a few possible kinds of solution.... In the design of a bridge there are in fact three elements: the classes possible in this universe, the unique properties of the materials available for its construction; and the engineer only takes third place by selecting the class of solution, and by utilising the properties of his materials to achieve the job in hand.... Like the engineer natural selection takes third place by giving reality to one or other of a series of possible structural solutions with the materials available. (Pantin, 1951, pp. 44–45)

Discussions with Pantin helped me to apply these insights to the functional or adaptive evolution of brachiopods; the notion of intrinsic limitations on the variety of designs capable 'in this universe of ours' of fulfilling any specific function, given 'the unique properties of the materials available', was particularly attractive. I first publicly used Pantin's ideas on organic design when I made a series of plaster models (for clarity, far larger than life) for a formal 'conversazione' at the Geological Society in London in 1957, marking its 150th anniversary, and then for two similar events at the Royal Society in 1958; that I was invited to contribute in this way was a direct result of Bulman's patronage. The display was on 'Some functions of the "ornament" on fossil brachiopods'. The term 'ornament' was used frequently by pale-ontologists at this time, for example to describe minor surface features of fossil shells, with the implication and usually unargued assumption that they were non-functional and without adaptive value. I claimed that my models showed how some such features of fossil brachiopods

could instead be interpreted as adaptive 'devices for excluding large foreign particles from the mantle cavity' when the valves were gaping apart and the current system was in operation. I explained the significance of this in the program for the event:

> There are only three ways in which a brachiopod could be protected from the entry of such particles: by having (1) a *mesh* or (2) a *grille* over the aperture, or (3) by having the aperture in the form of a long narrow *slit*. In addition to this fundamental limitation, the possible range of structures is further restricted by the brachiopod's anatomy: e.g., the bars of a grille can only be formed of spines [i.e., projections of shelly material] or setae [fine bristles of organic material, which are embedded in the tissue around the edges of the valves in most living brachiopods]. Thus, since there are relatively few possible ways of protecting the aperture, it is inherently probable that each kind of device was developed more than once in the course of brachiopod evolution. (Geological Society, 1957, p. 6)

After I showed these models at the Royal Society I was asked to write an article making the same point for the then recently founded *New Scientist*, a rather modest British equivalent of *Scientific American*; this usefully got my ideas a much wider scientific audience (Rudwick, 1958). The following year Bulman, as president of the geology section of the British Association, reviewed 'Recent developments and trends in palaeontology', stressing the importance and indeed the centrality of morphological studies. He ended his address by commenting that the *functional* morphology of fossil invertebrates was 'strangely neglected' in contrast to what Simpson, for example, had been doing with fossil vertebrates. He specifically cited my research as showing that functional inferences for fossils could in principle be *tested*. 'In fact,' he concluded, 'functional analysis of morphology in invertebrate fossils promises to become one of the most rewarding fields of investigation' (Bulman, 1959, p. 42).

The Paradigm Method in Action

Before publishing anything that might justify this highly encouraging comment, I tried to improve my first-hand knowledge of living brachiopods, which—as in Nichols's work on fossil sea-urchins—were obviously an indispensable key to the functional interpretation of fossil forms, but about which published observations were still sparse and in

some cases unreliable and misleading. In 1959–1960, during a lengthy visit to New Zealand, where most unusually three diverse genera were easily accessible in intertidal rock pools, I was able to make observations that later added to the very few published accounts of brachiopod suspension-feeding (Figure 1).

These observations confirmed my previous *predictions* about the natural disposition of the lophophores and the courses of the water currents they generated. This greatly strengthened my confidence in the functional reconstructions I had already made for various extinct brachiopods. More intangibly, many days and weeks spent watching individual brachiopods living their unspectacular lives undisturbed gave me a strong but indefinable 'feeling for the organism'. This extended to the point of occasionally finding myself dreaming of *being* a brachiopod: an experience—anticipating Thomas Nagel's later and famous philosophical question, 'What is it like to be a bat?'—that it might have been professionally imprudent to disclose at the time, but which half a century later I can acknowledge as having been both experientially vivid and heuristically invaluable.

Before visiting New Zealand, I chose one of my cases of fossil functional morphology as one of the first portions of my dissertation to publish; the paper appeared in the *Geological Magazine*, a highly respected research journal although, significantly, not a biological or even primarily paleontological one (Rudwick, 1960). The case was that of two major extinct groups of brachiopods (*spiriferides* and *atrypides*)—very few of which survived the end of the Palaeozoic era—in which the lophophore took the form of a pair of helical spirals; their form is preserved in the fossils as a pair of delicate shelly spirals, which evidently supported the suspension-feeding structure in the living animal. I used the structure and function of spiral lophophores in living brachiopods as a *homological* clue (it was confirmed by my work in New Zealand just in time to be referred to in the published paper). I argued that the basic requirement for any 'ideally efficient filter-feeding [or suspension-feeding] current system' in brachiopods was that, in order to avoid wasteful recycling or multiple filtration, the lophophore must divide the mantle cavity in such a way that water as yet unfiltered is kept separate from filtered water, the respective 'inhalant' and 'exhalant' chambers' having their own separate 'apertures' at the edge of the shell when the valves gape apart. As an *analogical* clue, there was plenty of published evidence that this specification was observably fulfilled not only by the susension-feeding systems of all living brachiopods but also by those of many other unrelated organisms. Echoing Pantin's ideas, I
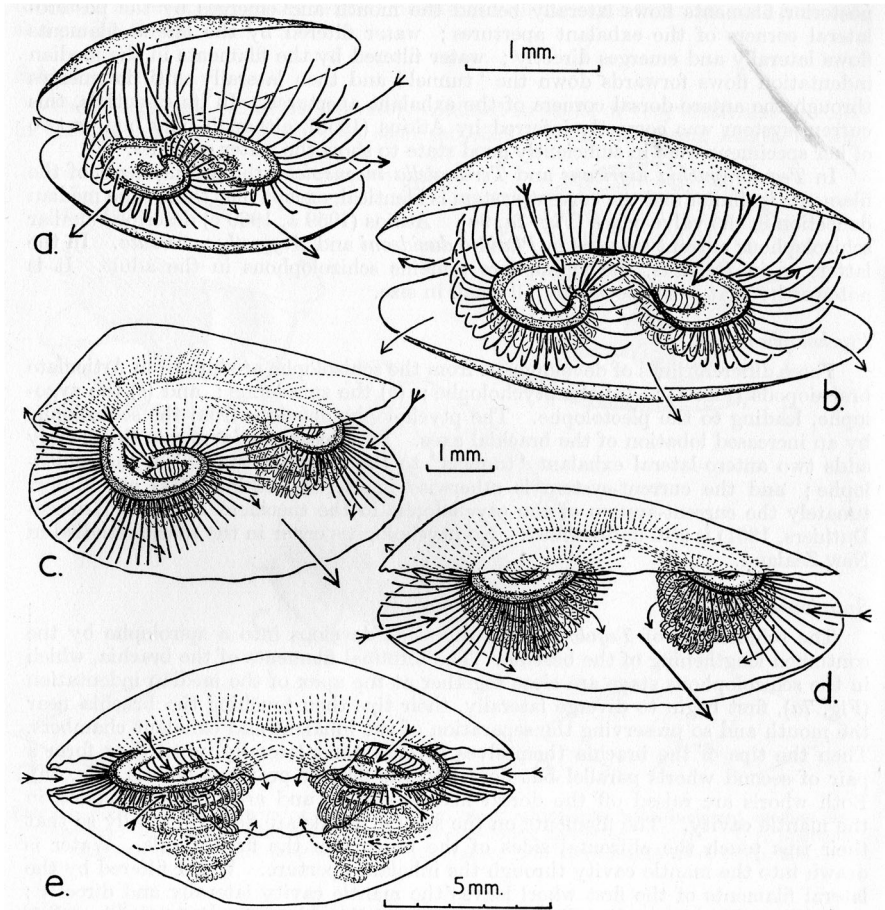
Figure 1. Drawings of living individuals of the brachiopod *Tegulorhynchia*, showing their spiral lophophores and the water-currents they generate at successive growth stages (Rudwick, 1962, Figure 7). The larger shells were depicted as if transparent, in order to show parts of the lophophore visible through the gape between the valve edges when viewed from other angles. The coiled linear axes of the lophophore bear a row of ciliated 'filaments' (here shown, for clarity, much more widely spaced than they are in reality) that collectively form an area of filter. The elaboration of the lophophore during ontogeny, with the progressive enlargement and complexity of the spirals, is clearly related, as a dimensional effect, to the increasing size and volume of the living organism. For clarity's sake these drawings omitted the '*grilles*' of slender sensitive setae (or chaetae), projecting from inside each valve edge, which effectively protected the animal by triggering the shell to snap shut if touched by a potential predator

argued that only two alternative arrangements of a spiral lophophore were topologically possible to achieve the necessary spatial division of the mantle cavity, the interiors of the spirals being parts of either the

inhalant or the exhalant chamber. It followed that both alternatives almost certainly evolved independently several times. This conclusion was supported by the inference that each was found in quite diverse taxonomic groups (Figures 2, 3).

I claimed that this reconstruction of the suspension-feeding of these extinct brachiopods was much more plausible than one that had been proposed by Alwyn Williams (1921–2004), a more senior British brachiopod specialist (Williams, 1956, pp. 269–271). I argued that Williams's reconstruction was *homologically* incompatible with the known anatomy of living brachiopods, *topologically* impossible on any conceivable arrangement of the lophophore, and *hydrodynamically* inefficient. In a subsequent exchange, Williams defended his reconstruction, but I claimed in response that it 'ignores the basic prerequisite of functional efficiency' (Williams and Rudwick, 1961). Williams's further
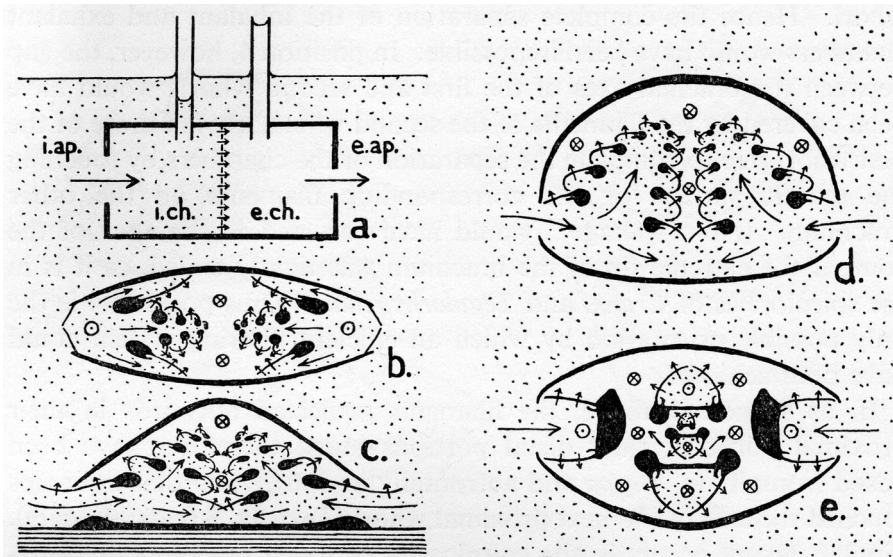
Figure 2. A diagram (Rudwick, 1960, Text-Figure 7) of 'an ideally efficient filter-feeding [or suspension-feeding] current-system' (*a*), with an active filtering partition pumping water from an 'inhalant' into an 'exhalant chamber' (*i.ch., e.ch.*), each with its separate 'aperture' (*i.ap., e.ap.*). The other drawings (*b—e*) represent cross-sections of four genera of *living* brachiopods, interpreted as varied embodiments of this 'ideal' system (*d* is *Tegulorhynchia,* shown more naturalistically in Figure 1). Each brachiopod is illustrated by a cross-section of the two shelly valves, the mantle cavity and lophophore between them, and the observed laminar flow of water-currents (unfiltered water is stippled; the cross-in-circle symbols represent currents flowing perpendicular to the cross-section, mostly towards an exhalant aperture at the front of the gaping shell)
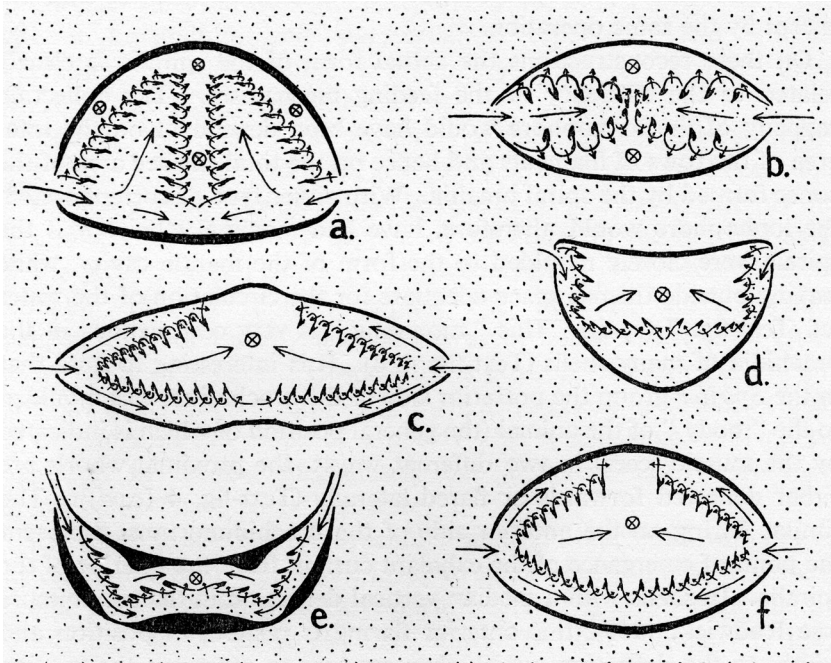
Figure 3. My first published functional reconstruction of fossil brachiopods (Rudwick, 1960, Text-Figure 8): six *extinct* genera of brachiopods (*a—f*), with their inferred current-systems shown for comparison with living genera. Only two arrangements of spiral lophophores are topologically possible as embodiments of the 'ideal' system, with the interiors of the spirals filled with either unfiltered (inhalant) or filtered (exhalant) water. In both living and fossil examples, the lophophore is or was clearly moulded to the varied shapes of the mantle cavity within the shell: this would advantageously maximise the *length* of the lophophore and the *area* of its filtering apparatus within the space available

elaboration of his argument revealed more clearly that his reconstruction entailed a *double* filtration of the water passing through the system (Williams and Wright, 1961, pp. 172–176), which in my view made it intrinsically very inefficient. Williams's unrealistic depiction of the filaments on his reconstructed lophophore also suggested to me that my critic had never had an opportunity to watch the suspension-feeding system of any living brachiopod in undisturbed action (most published descriptions of brachiopod anatomy were based on preserved specimens, in which the lophophore is usually shrunk and distorted).

The Paradigm Method Defined

In 1959, shortly before leaving England to study living brachiopods in New Zealand, I had given a lecture to the geology section of the British Association, posing the basic palaeobiological question, 'How can we hope to reconstruct the life of an extinct animal from its fossil remains?' A comparison with related living species was obviously the most effective way to start; but 'if *no* living animal resembles the extinct one at all clearly', the problem was more difficult:

> The only alternative is to study the fossil as though it were a *piece of machinery of unknown purpose*. We can analyse its construction to see what sort of life the animal *could* have followed successfully, in other words to see what *sort* of activities its structure would have allowed it to do. This is rather like studying the mechanism of an unwound clock, without having any idea what clocks are for. It would be possible—though probably not easy—to hit upon the right answer, and to realise that if the clock were wound up the hands would mark the passage of time accurately, but would be pretty useless for doing anything else. (Rudwick, MS dated 7 September 1959).

This teasing allusion to the famous (or notorious) rhetorical starting point of Paley's 'argument from design' introduced my functional analysis of some very strange fossil brachiopods; it was this specific example that evoked Bulman's approval in his presidential address at the same meeting, and his prediction that functional morphology was an area of great promise in paleontology.

My work on this difficult case of functional interpretation was submitted, shortly before my visit to New Zealand, as a long and densely illustrated paper for *Palaeontology*. 'The feeding mechanism of the Permian brachiopod *Prorichthofenia*' (Rudwick, 1961) was in fact the very first paper in that journal to express in its title an author's intention to interpret fossils in terms of functional morphology. The fossils known collectively as 'richthofeniids' had long been known from Permian (late Paleozoic) rocks in many localities around the world. They were recognized as brachiopods of highly unusual form, but many features of their morphology were puzzling or obscure. In the 1950s, however, Cooper—not only a prominent American paleontologist but more specifically one of the world's leading experts on brachiopods—had begun to report on those he was extracting from Permian limestones in the Glass Mountains of west Texas. These rocks

were turning out to be almost as significant as *Lagerstätten* such as the Burgess Shale (which preserves 'soft-bodied' organisms), because at some time in the deep past the calcareous 'hard parts' of many fossil organisms, including the shells of a vast array of brachiopods, had been naturally replaced by silica, accurately in every detail. Large blocks of rock, immersed in baths of acid to dissolve the surrounding limestone, were yielding huge numbers of 'silicified' fossils that were astonishingly well preserved. Cooper, as head of the department he later redefined as 'Paleobiology', arranged for samples to be sent to other leading institutions. One such collection of specimens from the Glass Mountains went to the Sedgwick Museum in Cambridge, where I was able to study them. Cooper and his younger collaborator Richard Grant (1927–1995) were not expected to complete their huge monograph on the Glass Mountains brachiopods for several years (they duly did so, over a decade later: Cooper and Grant, 1972–1977). Bulman therefore approved my proposal to publish a study of the functional morphology of some of them, since this was clearly complementary to, and not competitive with, the Americans' more conventionally taxonomic approach.

At the start of my paper, I explained my proposed method for inferring functions from structures in extinct organisms. Here I used the word '*paradigm*' publicly for the first time in this context, to formalize the concept of 'ideally efficient' functional features. The brief methodological introduction to the paper became the *locus classicus*—often cited by others, approvingly or not, in subsequent years—of what the 'paradigm method' was intended to achieve, so it is worth quoting it here in its entirety:

> Many functions of the body demand, for their efficient operation, predictable modifications of the anatomy. For these, it is often possible to specify the nature of the 'ideal' structure that would be able to fulfil this function with perfect efficiency. But in actuality the materials (anatomical and environmental) are never 'perfect' in their properties. For any given set of materials, the 'ideal' structure must, therefore, be modified into the *paradigm*. This is the structure that can fulfil the function with maximal efficiency under the limitations imposed by the nature of the materials. The degree of approximation between any paradigm and an observed fossil structure is a measure of the efficiency with which the structure would have been physically *capable* of fulfilling the function; but it cannot establish the probability that the structure *did* fulfil it. But by analogy with adaptation in living animals, there are strong grounds for inferring that a fossil structure capable of fulfilling a certain function with great efficiency

did fulfil that function, especially if it can also be shown that the structure would have been inefficient or inoperable as the agent of any other conceivable function. Thus, by transforming rival possible functions into their respective paradigms, rival structural predictions can be made; and these can be tested by direct comparison with the observed structure of the fossil.

The ease and confidence with which a function can be inferred by this method is directly proportional to the efficiency of the adaptation. A structure that was very efficient will approximate very closely to the paradigm of its function, and thereby can be recognised as an adaptation with relative ease. A less efficient structure will be more ambiguous, because it will not be very similar to its paradigm, and is likely to show some points of resemblance to the paradigms of other functions. A non-adaptive structure can never be recognised as such; for its apparent lack of correspondence to any paradigm might always be due to failure to consider the correct function and the correct paradigm. Thus there can be positive and cumulative evidence that a structure was an efficient adaptation; but it is methodologically impossible ever to demonstrate that a structure was non-adaptive.

This method involves an analysis of adaptation only as a static phenomenon. Theories of its causal origin (e.g. by natural selection) or of its temporal origin in a particular instance (by a particular evolutionary lineage) are irrelevant to the detection of an adaptation (Rudwick, 1961, pp. 450–451).

This set out explicitly the method that had been implicit in my reconstruction of spiral lophophores in extinct brachiopods, and the highly efficient suspension-feeding current systems that they could have made possible. In this new case, however, the method faced a much greater challenge, to make functional sense of morphological features unlike those of any living brachiopods.

Prorichthofenia, two distinct species of which were analyzed, was radically unlike any living brachiopod or most fossil ones [the species will be referred to here by the names they bore at the time; *P. permiana* and *P. uddeni* were later assigned by Cooper and Grant (1969) to separate new genera]. Externally the shells had the form of a cone of highly irregular and variable shape, cemented to some hard substrate at its apex and often also by external spines that had clearly functioned as stabilizing struts. Recessed within the cone was a thin flat plate, hinged

on one side like a trapdoor, and preserved in different positions that clearly represented a wide angle of movement in life. Projecting from the internal walls of the cone were shelly spines: in *P. permiana*, an irregular *thicket* of stout spines covering much of the opening of the cone above the trapdoor; in *P. uddeni*, a *grille* of slender spines, joined up in some specimens to form a more or less complete and regular *mesh* in the same position; in both species there might also be a thicket of irregular spines on the under side of the trapdoor (Figure 4).
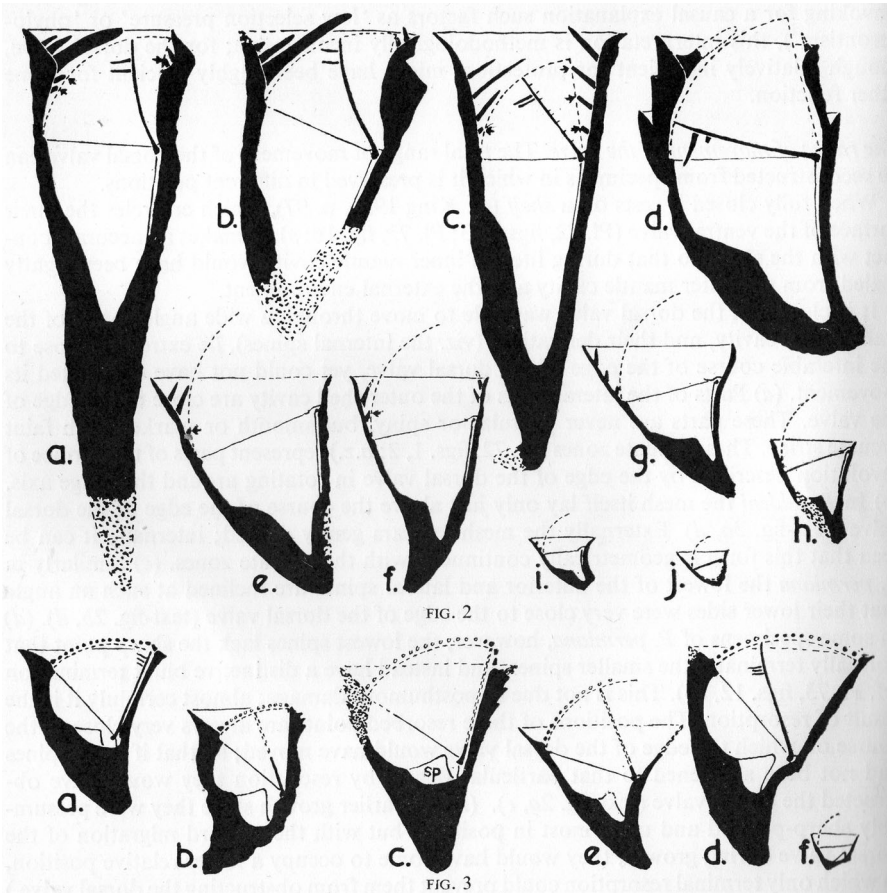
Figure 4. Vertical sections through specimens of *Prorichthofenia permiana* (upper rows, *a–h*) and *P. uddeni* (lower row, *a–f*), showing the thin trapdoor hinged on one side and preserved in various positions but evidently able to rotate through almost a right angle (Rudwick, 1961, Text-Figures 2, 3). Just clear of its arc of movement are thickets of spines in *P. permiana* and a more or less complete mesh (shown as an arc of dots) in *P. uddeni*; there is also a smaller thicket of spines on the under side of the trapdoor in both species. The smaller specimens, probably juveniles, have no spines

In contrast to this bizarre morphology, the hinge and the attachment scars of muscles were comparable to those of some more 'normal' fossil brachiopods (particularly the *productides*, a large and diverse group in the later Paleozoic). These features left no doubt that *Prorichthofenia* was indeed a brachiopod, and that the trapdoor and the cone were respectively its dorsal and ventral valves. Other details, however, left little doubt that in *Prorichthofenia* the thin tissue that lines the mantle cavity in living brachiopods must have extended far beyond the dorsal valve. In life it must have been permanently exposed, covering the internal surfaces of the outer parts of the conical ventral valve and all its spines or mesh (and probably also the outer surface of the dorsal valve). These inferences provided the homological foundation for my functional analysis (Figure 5).

Several puzzling anomalies in the morphology of *Prorichthofenia* led me to propose an equally unusual functional interpretation. One such anomaly was the disparity between the dorsal valve—the thin and delicate trapdoor—and muscle scars that indicated musculature at least as powerful (relative to the size of the animal), if not more so, as that of
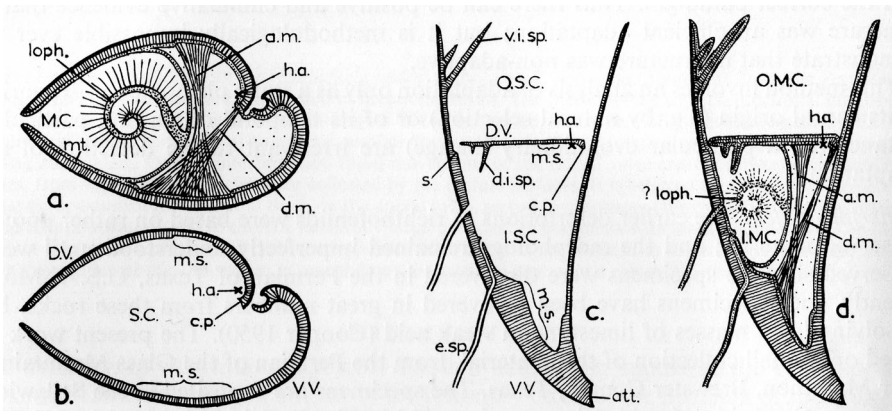
Figure 5. 'Homological relations between a "normal" brachiopod (*a*, *b*) and a richthofeniid (*c*, *d*)': a living brachiopod with its observed anatomy (*a*) and its 'hard parts' preserved in fossils (*b*), compared with the 'hard parts' of the fossil *Prorichthofenia* (*c*) and its anatomy inferred by homology (*d*). (The stippling denoted the 'body' of the animal, occupying only a part of the space between the dorsal and ventral valves, *D.V.*, *V.V.*). Muscle scars (*m.s.*) like those of less aberrant forms allowed a reconstruction of the familiar brachiopod system of leverage around the hinge axis (*h.a.*), powered by antagonistic muscles (*a.m.*, *d.m.*). Note the thin 'mantle tissue' lining the mantle cavity of the living brachiopod; and its inferred extension in the fossil, far outside and beyond the trapdoor, to line the whole interior of the cone (Rudwick, 1961, Text-Figure 1)

much less aberrant brachiopods. Added to this was a hinge mechanism clearly homologous with that of those other brachiopods, but looking in detail astonishingly like a piece of precision engineering that would have enabled the trapdoor to rotate easily through almost a right angle (Figure 6).

I suggested that the peculiar morphology of *Prorichthofenia* could be interpreted in functional terms as having served an equally unusual feeding mechanism. Contractions of the two antagonistic sets of muscles would certainly have been capable of opening and closing the dorsal valve, just as in living brachiopods, and in this case through a wide angle. The closing movements might have been very rapid, again as in living brachiopods, and possibly the opening movements too. These movements could have swept currents of water alternately in and out of the interior of the conical ventral valve, perhaps rapidly. If so, suspended particles might have been captured in some way and used as food (in the absence of any preserved evidence, the form of the lophophore was left unspecified).

This line of reasoning obviously graduated from the mechanically certain through the homologically possible to the functionally conjectural. But I argued that it could be *tested* by experimentally simulating the putative flow of water currents in and out of the reconstructed brachiopod. I therefore made a working model of *Prorichthofenia* (at natural size, to avoid dimensional complications) in which the trapdoor (of thin transparent plastic) could be alternately opened and closed at varying speeds (by fine threads positioned to replicate the muscles). When the model was immersed in water, the resultant currents (made visible by a suspension of oil droplets, brightly illuminated) could be
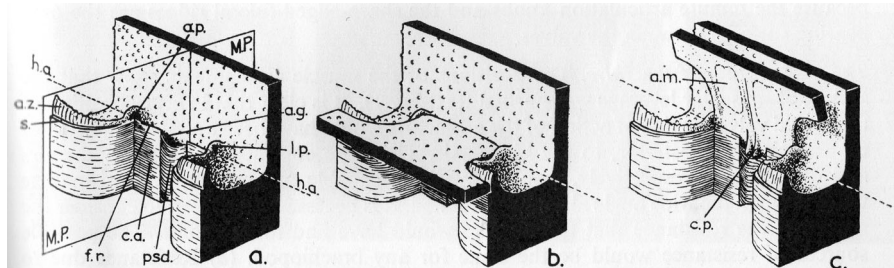

Figure 6. 'Hinge structure of *Prorichthofenia*, shown by block diagrams (cut edges of valves shown in solid black)' (Rudwick, 1961, Text-Figure 4). The dorsal valve was pivoted on a knife-edge fulcrum (*f.r.*) and held in place by a pair of knobs fitting into corresponding sockets; as in less aberrant brachiopods, it could have been opened by muscles attached to a projection (*c.p.*) at the back of the dorsal valve and just behind the fulcrum

watched and filmed in action, at any desired speed. The results of these experiments far exceeded my expectations: the complex hydrodynamics of the turbulent flow patterns showed for example that the thickets of spines in *P. permiana,* and those under the dorsal valve of both species, were optimally situated to intercept the currents and hence potentially to catch suspended food particles (Figure 7).

This '*flapping*' mode of operation (as it was later called) made functional sense of many apparently minor details of the morphology. For example the stout spines on *P. permiana* were in a thicket which would have ensured the turbulence of the passing currents. If the thin mantle tissue that must have covered (and indeed formed) them was both ciliated and secreting mucus (as in living brachiopods), this could have maximized their efficiency as a device for intercepting and trapping suspended food particles and then conveying them to the mouth. In contrast the spines on *P. uddeni* were slender and streamlined in profile, in a single row forming a grille, or further elaborated into a complete mesh with apertures of strikingly uniform size, which would have maximized their efficiency as a protective device while minimizing their hindrance to the currents. This one morphological feature, in these two
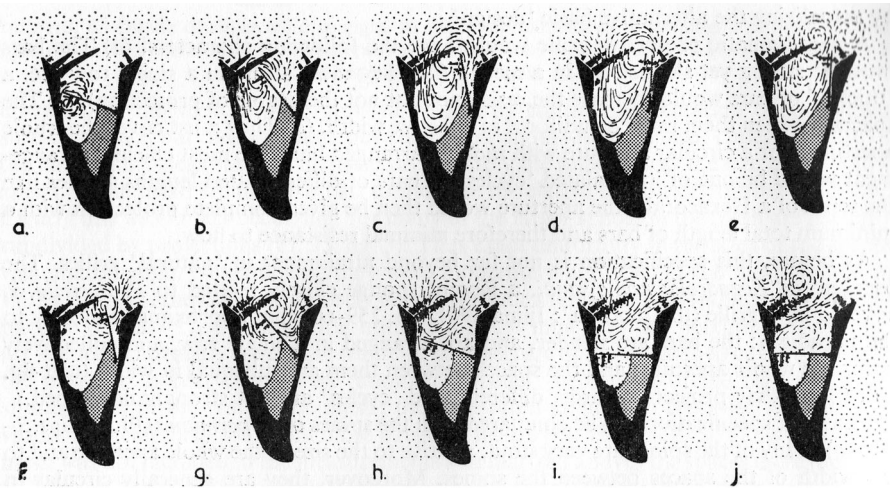

Figure 7. A reconstruction of the turbulent water currents and eddies that would have flowed in and out of a *Prorichthofenia permiana* when the delicate 'trapdoor' dorsal valve was opened (*a—e*) and closed (*f—j*) fairly rapidly (Rudwick, 1961, Text-Figure 8). The currents shown were based on filmed sequences, also published, of a working model in operation. A matching set of diagrams showed the currents and eddies in *P. uddeni*, with its delicate 'mesh' protecting its interior from potentially harmful large particles. (The regular stippling denotes the inferred 'body' of the animal.)

species, could therefore reflect differential adaptations within a common 'flapping' mode of operation, with the spines serving primarily either as a food-collecting or as a protective device.

The plausibility of this putative mechanism was supported for example by the somewhat similar mode of feeding—a forceful pumping mechanism—known in living septibranch molluscs. I noted briefly how it might have developed in ontogeny, from simpler arrangements in juvenile stages of *Prorichthofenia*; and in phylogeny, from more conventional feeding mechanisms in related but less aberrant brachiopods. But the primary emphasis was on the ways in which any mature individual richthofeniid might have operated in life. The interpretation was based on considerations ranging from the strictly mechanical and almost irrefutable (given the preserved 'hard-part' morphology), through what was probable on homological grounds (given the known basic anatomy and physiology of living brachiopods), to the unavoidably conjectural and yet plausible (in the light of analogues among other unrelated organisms). In summary, my emphasis was on the inferential efficiency of the entire morphology to make possible a feeding mechanism without parallel in modern brachiopods: either a regular rhythmic flapping of the dorsal valve, or else at least an intermittent or occasional rapid movement (perhaps triggered by the sensed proximity of potential food particles, as in septibranchs). However, rather surprisingly, this comprehensive functional interpretation of a strikingly aberrant organism made only occasional reference to my key concept of paradigms, except in the paper's brief opening methodological statement.

One initial reaction to this paper was a significant indication of the then status, among more senior paleontologists, of any such paleobiological study. An anonymous report for *Palaeontology*—from internal evidence I guessed it was by Cooper's British counterpart Helen Muir-Wood (1895–1968), the brachiopod specialist at the British Museum (Natural History) in London, whom I had already encountered in person—recommended that the paper be rejected, and submitted instead to some *zoological* journal (Norman Hughes to Rudwick, 28 October 1959). This was a notable sign of how the science of paleontology was implicitly defined, or circumscribed, at this time. The same report also deplored my proposed use of an expensive collotype plate to reproduce stills from the ciné films of my working model: images not of any real fossil specimens! Fortunately the editor of *Palaeontology* ignored this report—another may have been more favorable—and the paper was accepted for publication.

What Cooper initially thought of this paper is uncertain. I had first met him in Washington when returning from New Zealand and while the paper was in press. Cooper had briefly shown me some of his spectacular Glass Mountains specimens and given me unlimited access to the rest of the Museum's rich brachiopod collections; but he had seemed sceptical about any *functional* interpretation of morphological features that for him were essentially of taxonomic and phylogenetic significance. In contrast, at least one paleontologist with a different perspective was more positive: Ager, in his *Principles of Paleoecology*, summarized my paradigm method, judged that the feeding mechanism attributed to *Prorichthofenia* was plausible, and approved the interpretation of the mesh of spines in *P. uddeni* as a protective device (Ager, 1963, pp. 59, 66–67).

The Paradigm Method Extended

Ager also noted that another kind of protective device for brachiopods had already been suggested by Herta Schmidt (1900–1992), a paleontologist working in Frankfurt-am-Main. Although her paper had been published in the Senckenberg Museum's own journal rather than in *Palaeobiologica*, Schmidt's 'Zur Morphogenie der Rhynchonelliden' (Schmidt, 1937) was a fine example of the pre-war German tradition of *Paläobiologie*, applied to a specific group of brachiopods from a specific geological period and region (the Devonian of the Eifel). Schmidt had shown that some of these fossil species developed valve edges of strongly and sharply zigzag form, such that when the shell opened there would have been a lengthy narrow zigzag slit into the mantle cavity rather than a wider unprotected gape; when, during life, the valves had gaped apart for the feeding system to operate, this could have prevented harmfully large particles from entering the mantle cavity. Since no living brachiopods have zigzag valve edges, this functional reconstruction was only slightly less problematic than my later interpretation of the more aberrant richthofeniids.

I had already used Schmidt's work in my dissertations and for my exhibited models, but I developed it further in another lengthy and densely illustrated paper in *Palaeontology*, on 'The function of zigzag deflexions in the commissures of fossil brachiopods' (Rudwick, 1964a). This extended Schmidt's functional interpretation to cover all brachiopods, of all geological periods, in which the line (the '*commissure*') along which the valve edges meet was modified or 'deflected' during the

accretionary growth of the shell into a sharply zigzag form. I argued that Schmidt's suggestion could be *tested* by comparing these zigzags with the form that would be, as nearly as possible, the *paradigm* for the proposed function. This would be a zigzag that would, as nearly as possible, produce *a slit of uniform width* all round the valve edges. This would depend solely on the three-dimensional form of the valve edges (which is preserved in the fossil shell) and not at all on the angle of gape when the shell was open in life (which could not be observed or known with any certainty). At its geometrically simplest, zigzag valve edges perpendicular and parallel to the hinge axis would necessarily have specifiable forms, for any given 'wavelength' and 'amplitude' of zigzag (Figure 8).

In the case of any real brachiopod shell, these geometrically ideal forms would have to be modified, to allow for the fact that the valve
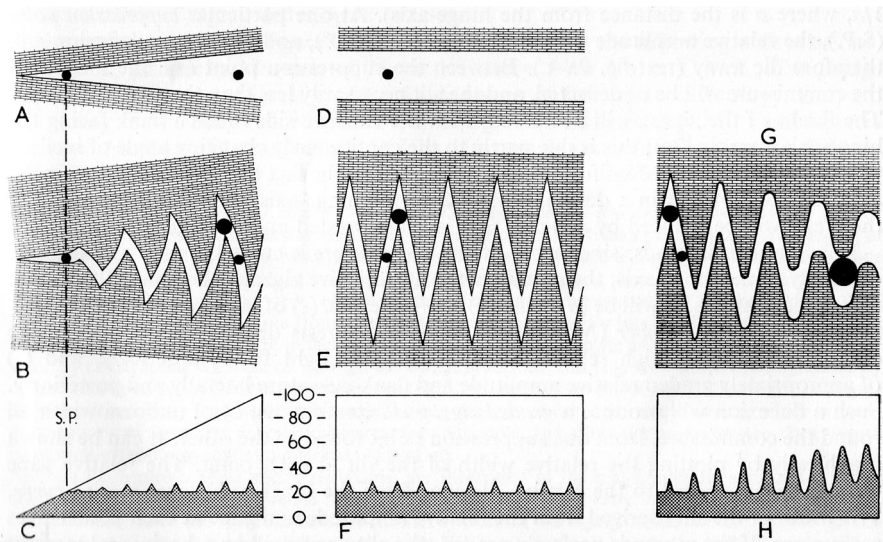
Figure 8. The basic 'paradigm for protective zigzag slits', with potentially harmful large particles represented schematically (as they were by Schmidt) as spheres of different sizes (Rudwick 1964a, Text-Figure 2). This diagram set out the basic geometry, with arbitrarily chosen 'wavelength' and 'amplitude' and any small angle of gape. A–C represented valve edges perpendicular to the hinge axis; D–F, parallel to the hinge axis. A and D represented valve edges unmodified; B and E, valve edges modified into zigzag form. C and F showed maximum sizes of particles that could pass through each point in the zigzag slits, relative to the total gape; note the small anomalies represented by the slightly less well protected crests of the zigzags, and the 'suppression point' (S.P.) near the hinge axis where the wave form dies away and the gape narrows to zero. The effectiveness of the protection also depended geometrically on the sharpness of the zigzags (G, H)

edges are only locally perpendicular or parallel to the hinge axis, because they are usually subcircular or elliptical in plan. The geometrical ideal would therefore have to be modified into a set of more realistic paradigms covering a range of related specifications. All of these would yield a slit of precisely uniform width when the valves gaped apart; but the exact form that the paradigm took would depend on the overall shape of the valve edges, the 'wavelength' of the zigzag, and the 'amplitude' of the zigzag at its maximum furthest from the hinge axis (Figure 9).
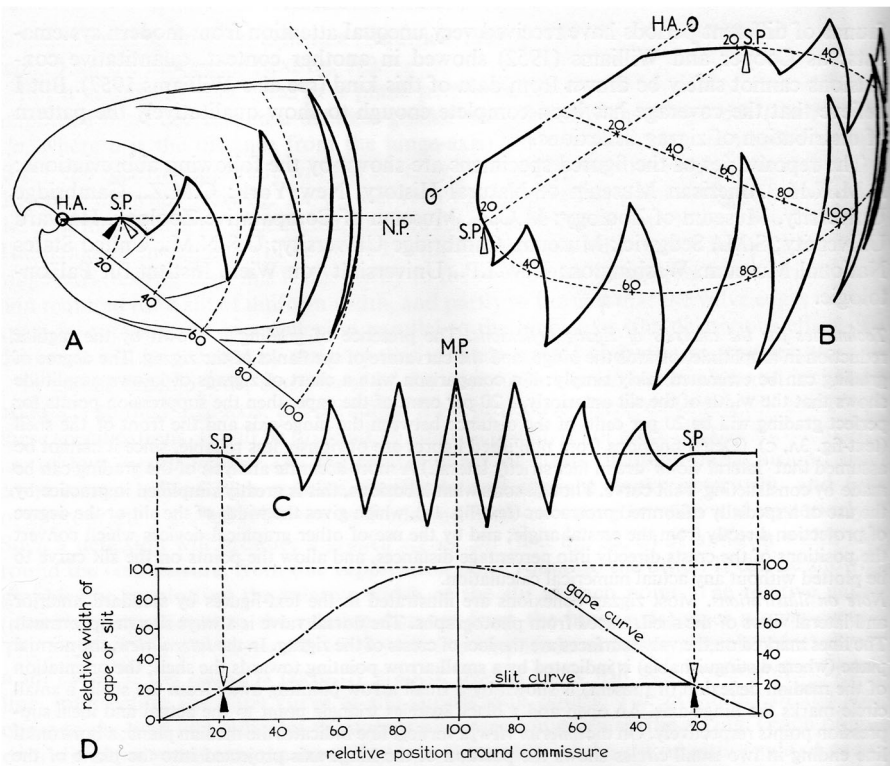
Figure 9. The 'paradigm for [a] protective zigzag deflexion', for the case of a brachiopod shell with the most common form (subcircular in plan and biconvex in profile), and with arbitrarily chosen 'wavelength' and 'amplitude' (Rudwick, 1964a, Text-Figure 3). The resultant zigzag form of the valve edges is shown in lateral profile (A), in perspective (B), and 'unwrapped' into a linear form (C); it has sharp crests, and flanks that are distinctively arcuate in three-dimensional form. When the valve edges gaped apart through any small angle, this geometrical form would necessarily produce a slit of precisely uniform width, as shown by the uniform 'slit curve' (D), except near the hinge and (not shown here) at the crests of the zigzag

The putative function of zigzag valve edges, as a protective device, could then be *tested* by comparing these paradigm forms of zigzag—adapted to match any given shell shape—with the forms found in reality on fossil brachiopod shells. Having searched museum collections for exceptionally well-preserved specimens from many stratigraphical levels and many parts of the world, I published accurate drawings (and photographic details) of brachiopods with zigzag valve edges, belonging to many of the main taxonomic groups defined by brachiopod specialists (Figure 10).

What was remarkable and unexpected about this wide-ranging survey of brachiopods with zigzag valve edges was that in many cases their valve edges were strikingly close to the paradigm, with its strongly arcuate form and the distinctive way the 'amplitude' of the zigzag died away when traced towards the hinge axis. This proved—*with certainty*, as a matter of three-dimensional geometry—that when in life the valves gaped apart through any small angle, there would have been *a slit of uniform width* between the valve edges all round the shell. As a further and interpretative step, it could then be inferred that this uniformly
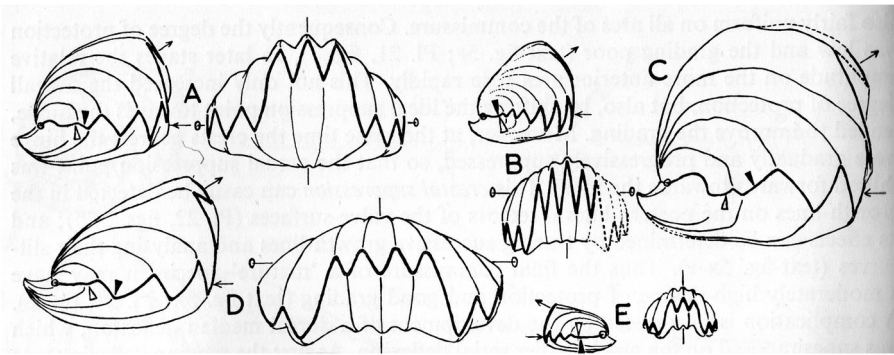

Figure 10. Shells of five fossil brachiopod species (depicted as accurate drawings of anterior and lateral views, traced from photographs or by camera lucida), with zigzag valve edges of varying degrees of approximation to their respective paradigm forms (indicated on the lateral views by the proximity of the ideal and actual suppression points, marked respectively by black and white pointers). On these particular shells the median parts of the valve edges are further deflected relative to the lateral parts, which I interpreted as a likely separation of a median exhalant aperture from lateral inhalant ones (both shown on the lateral views by small arrows), which would have reduced the chance of external recycling of the water. These particular species were all Mesozoic in age and all belonged to one taxonomic group (*rhynchonellides*); but other sets of drawings depicted similar zigzag forms on species ranging through much of the Phanerozoic (from Ordovician through Cretaceous) and belonging to many different major groups, making it almost certain that zigzag forms evolved many times independently (Rudwick, 1964a, part of Text-Figure 6)

narrow slit could have functioned efficiently *as a protective device* to exclude potentially harmful 'particles'—say, predators or parasites or floating debris larger than a certain critical size—from entering the mantle cavity: either by acting simply as a physical barrier, or by triggering the highly sensitive tissue lining the valve edges to cause the shell to snap shut (the efficacy of this reaction had greatly impressed me while I was watching living brachiopods over long periods). This functional interpretation was further supported by the fact that, as Schmidt had shown, in a few fossil species even the intrinsic 'imperfection' represented by the lesser degree of protection at the crests of any zigzag (Figure 8B, E) was eliminated by the development of slender spines of shell material just inside the valve edges *at precisely these points*. And there was indirect evidence that in other species the same 'imperfection' at every crest of any zigzag had been covered in the same way by a bristle-like seta (not normally preserved) in exactly the same position. All this showed 'organic design'—or adaptation—at an astonishing level of precision.

Up to this point, my analysis of zigzag valve edges was focused on their final form in the mature shell. But in reality brachiopod shells grow throughout ontogeny by accretion at the valve edges, and all the preceding external forms of the shell are preserved and visible in its growth-lines; the implications of this, not always adequately recognized at the time, had already been set out in my first published research paper, on 'The growth and form of brachiopod shells' (Rudwick, 1959), a title that deliberately echoed D'Arcy Thompson's great work. These records of the growth of the shell made it clear that in each case the zigzags had developed quite gradually by the modification of pre-existing deflections in the valve edges, deflections that were less accentuated and less sharply zigzag in form. In other words, a close approximation to the paradigm only developed late in ontogeny. And since many other brachiopod species showed similar ontogenetic pathways without finally developing any strong zigzags, this suggested that in them the protective function had simply been less efficient or had been provided in other ways (perhaps, for example, by a grille of protruding setae). As further evidence for this protective function, a few specimens showed a healed injury to the valve edges (perhaps from a bite by a passing predator): traced in the growth lines, it was clear that this had been quickly repaired to seal the gape, and then further modified back into a form that restored precisely the degree of protection that had been lost, appropriate to that point on the valve edges.

In contrast, an alternative functional interpretation, which had been suggested by earlier paleontologists, could be rejected as highly unlikely: depending on the overall shape of the shell, zigzag valve *edges* did not necessarily generate a corrugated shell *surface*, and therefore would not always have strengthened the shell. Two alternative functions could thus be compared, and one was far more likely than the other.

This paper served to make the use of the paradigm concept more explicit than in my earlier paper on the feeding mechanism of richthofeniids. Specifically, it made clear the distinction between a theoretically 'ideal' structure and the *paradigm* that was as nearly ideal as was possible, given the anatomy—and evolutionary legacy—of the organism, out of which any adaptive structure had to be formed. The example of zigzags also showed that any paradigm did not necessarily apply to every feature at every stage of growth of the organism, nor did it imply that any given function was, or could be, fulfilled with perfect efficiency. Positively, however, using the paradigm method could lead to testable evaluations of rival functional interpretations. It could lead to a strong case in favor of one specific interpretation of a particular feature, as having been an effective adaptation within the limitations imposed by the relevant anatomy; and against another interpretation, which would have been demonstrably less effective or even useless. And what could be inferred confidently (at least in brachiopods, thanks to their accretionary growth) for the ontogenetic development of such features, could also be inferred for their phylogenetic history. In the case of zigzags in brachiopod valve edges, it was clear that they had developed by several different pathways during ontogeny, which made it highly likely that they had likewise evolved from various earlier forms without zigzags. Their wide taxonomic and stratigraphical distribution made it almost certain that protective zigzag slits must have evolved many times independently.

The further application of the paradigm method to other fossil brachiopods must be summarized here very briefly. One of the more significant cases was an analysis of the spiny Jurassic brachiopod *Acanthothiris* as having had an effective grille of shelly spines of strikingly paradigm form: long, slender, and spaced at uniform intervals all round the valve edges so as to cover the entire gape between the valve edges when the shell was open, while minimizing any obstruction to the water currents. The morphology of the tubular spines showed that they must have been formed by tiny offshoots of the sensitive edges of the mantle tissue; their tips would therefore have been in effect a uniformly spaced array of sensitive 'antennae', which could have given 'early

warning' of the approach of harmful agents from almost any direction (Rudwick, 1965a). Moreover, a potentially harmful object touching *any* of the spines could have triggered the usual reaction and snapped the shell shut, before it came near the apertures into the mantle cavity. Once again, geometrical certainty could be combined with homological probability to generate a plausible functional interpretation (Figure 11).

This case of a protective *grille* also exemplified, alongside zigzag *slits* and the exceptional (in brachiopods) *mesh* of *Prorichthofenia uddeni* and its relatives, all the three classes of protective device 'possible in this universe', which I had earlier identified—inspired by Pantin's analysis of organic design—and which I interpreted as making likely a large-scale pattern of evolution in which parallelism and convergence must have been widespread and even pervasive.
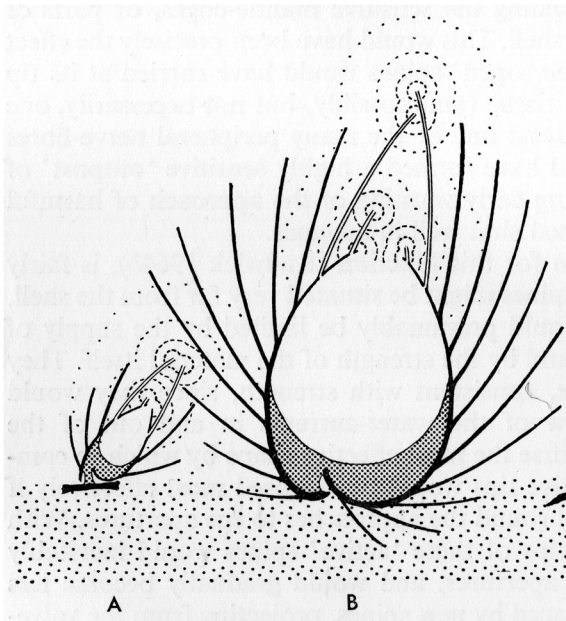
Figure 11. Reconstructions of a juvenile (*A*) and an adult (*B*) *Acanthothiris*, shown in section, with tubular spines formed at the valve edges at regular intervals during ontogeny (Rudwick, 1965a, part of Text-Figure 3). The most recently formed spines, not yet plugged by shell material, would have extended the sensitive mantle-edge tissue far out from the gape between the valve edges. This could have given 'early warning' (here depicted schematically by concentric contours) of the approach of potentially harmful objects. In addition, such objects, on touching *any* spine, could have triggered the shell to snap shut

The Paradigm Method and Evolutionary Theory

Meanwhile I expanded the brief methodological introduction to my earlier paper on *Prorichthofenia*, and applied it in a much wider context. My paper on 'The inference of function from structure in fossils' (Rudwick, 1964b) was not aimed primarily at other paleontologists; it was read at a meeting in London of the British Society for the Philosophy of Science and later published in its *Journal*. In deference to a distinguished philosophical audience—Karl Popper (1902–1994) was among those present—it focused on the paradigm method itself rather than on any specific instances of its application to fossil brachiopods. As its title implied, the basic problem was *epistemological*: how could we *know*—or, at least, infer on good grounds—that a structure had one function rather than another, if the organism was extinct and its functions unobservable?

However, this problem was set in the much wider context of the then current debates between 'Synthetic' or 'neo-Darwinian' evolutionary theory and its rivals such as 'orthogenesis' and 'typostrophism', as exemplified by arguments between Simpson and Schindewolf; and it focused on the crucial issue of adaptation. I argued that 'the organisms whose adaptive status we wish to evaluate [in order to test such theories] can only be recognised as such *in retrospect*'. It followed that 'the alleged ubiquity (or near-ubiquity) of adaptation can only be tested against the alleged existence of important non-adaptive features by referring to the evidence of palaeontology.' I took as an example the functional interpretation of the fossil 'pterodactyl' or pterosaur (showing incidentally that the fundamental problem was not confined to fossil invertebrates):

> All we need, ideally, is a knowledge of the operational principles involved in all actual or conceivable flight mechanisms possible in this universe. Consequently the range of our functional inferences about fossils is limited not by the range of adaptations that happen to be possessed by organisms at present alive, but by the range of our understanding of the problems of engineering…. This involves the limited 'teleology' that is inherent in any description of a machine as a machine…. Machines can only be described for what they are by referring to the way their *design* enables them to *function* for their intended *purpose*…. Of course, the 'purpose' implied in this is no more than the existence and survival of the individual organism, which from this point of view must be regarded as an end in itself; such a 'purpose' need not be evaded or

> concealed for fear of implying a Paleyan metaphysic. This fear probably accounts in part for the surprising neglect of functional inferences in palaeontology. (Rudwick, 1964b, pp. 33–34)

I claimed that, in fossil organisms that cannot be observed alive, likely functions can be inferred by comparison with the paradigms for those functions. A paradigm was again defined as '*the structure that would be capable of fulfilling the function with the maximal efficiency attainable under the limitations imposed by the nature of the materials*'[italics original]. An interpretation of any feature as having been adaptive could then be *tested* by comparing it with the relevant paradigm:

> Moreover, by transforming rival possible functions into their respective paradigms, rival structural predictions can be made; and these can be judged against one another by direct comparison with the observed structure of the fossil…. Our confidence in the result of this test will be cumulatively strengthened if we can show that it concurs with the results of similar 'risky' tests on other parts of the organism; if, in other words, we can gradually build up an intelligible reconstruction of the way in which the various organs interacted in the service of the whole organism to achieve a possible mode of life. (Rudwick, 1964b, p. 36)

To conclude this rather inadequate summary of a dense argument, I repeated the point I had made at the end of my earlier and briefer account, stressing an important limitation inherent in this proposed paradigm method:

> Functional inference involves an analysis of adaptation only as a static phenomenon. The perception of the machine-like character of the parts of an organism is logically independent of the origin of the structures concerned. Theories of their causal origin (e.g. by natural selection or by orthogenesis) and theories of their temporal origin (i.e. by a particular ontogenetic and phylogenetic sequence) are strictly irrelevant to the detection and confirmation of the adaptation itself. The functional reconstruction of fossils is thus logically unrelated to any and all evolutionary theories. (Rudwick, 1964b, p. 38)

This *methodological* exclusion of evolutionary considerations from my use of paradigms did not imply any reluctance to engage with issues beyond the elucidation of specific adaptations. On the contrary: in 1964 I was awarded my department's triennial Sedgwick Prize for a review of the whole brachiopod phylum, over its entire fossil record, in which I

tried to interpret all the animals' main functional systems—their feeding and protective mechanisms being just two of these—in terms of the repeated evolution of key adaptations. The award of a research grant then made it possible for my student Richard Cowen (1940–) to become my close collaborator, which thereafter greatly enlarged the scale of our joint research. It was eventually summarized in my short book, *Living and Fossil Brachiopods* (Rudwick, 1970)—much revised from my prize essay, and modeled on Nichols's *Echinoderms* (Nichols, 1962)—which integrated as closely as possible what was then known about living and fossil forms across the entire phylum. In this work Cowen and I used as our 'database' the then recently published volumes on brachiopods (Williams et al., 1965) in the huge international *Treatise on Invertebrate Paleontology* (Moore, 1955–1971), to which I had contributed the brief section on brachiopod ecology and paleoecology (Rudwick, 1965b); but in the absence of appropriate computer facilities we had to use traditional card-index methods for storing and sorting our interpretations of its voluminous data (it described some 1700 genera in 48 superfamilies).

Conclusion

By the mid-1960s my application of functional morphology to fossil brachiopods, and specifically my proposed method of 'paradigms', had been launched into paleontological debate, with many 'worked exemplars' published in detail. They were all drawn from the fossil record of a single zoological phylum; and an unimportant one at that, in the eyes of many biologists. But this could hardly obscure my belief that the same method could and should be tried out on invertebrate fossils of all kinds, and indeed on vertebrates too. Nor could the detailed character of my analyses of specific fossil brachiopods, latterly in invaluable partnership with Cowen, obscure our hope that such studies of functional morphology would contribute to a better understanding of major features of the history of life and its evolutionary interpretation. And my methodological essay, aimed at philosophers of science as well as our fellow paleontologists, showed how I hoped the epistemological implications of the paradigm method would be taken seriously by biologists more generally, and particularly by evolutionary theorists.

Among paleontologists, reactions to our studies of functional morphology in fossil brachiopods, and specifically to my proposed method of 'paradigms', ranged from the enthusiastic through the sceptical or unimpressed to the dismissive or even actively hostile, with a marked

generational dimension in which some senior figures seemed hardly to comprehend what was being suggested, even to refute it. I plan in a sequel to this article to trace these debates, and the fate of the concept of paradigms (paleobiological, not Kuhnian), through the following decade or two. Specifically, I shall suggest how the concept of *functional morphology*, as applied to fossils, was related to the '*theoretical morphology*' proposed by David Raup (1933–2015), and how both were subsumed within Seilacher's tripartite '*constructional morphology*'. I shall describe how Stephen Jay Gould (1941–2002), an increasingly prominent figure both within and beyond the world of paleontology, switched dramatically from enthusiastically endorsing the paradigm method to forcefully rejecting the 'adaptationist programme' that he claimed it embodied. I shall also describe how, at the same time, 'paleobiology' in the anglophone world shifted away from the original meaning of *Paläobiologie* and focussed instead on the computer-aided statistical analysis of the fossil record in the service of evolutionary theory (Sepkoski, 2005, 2012). This had the effect, however inadvertently, of marginalizing the earlier project of reconstructing and understanding the 'ways of life' of the past.

Acknowledgements

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