

He made the point that there was a clear progression through these four floras, from the Carboniferous cryptogams, through the gymnosperms of the Mesozoic and the angiosperms of the Tertiary, to the varied plants of the present day. He related this progression, and the parallel one he saw in the animal record, to the gradual decrease in the level of carbon dioxide in the atmosphere, with changing climate and sea-level also having a secondary effect (Bowler 1976, Ch. 2).

Early nineteenth century Britain

Stratigraphic work was being carried out in Britain, at about the same time as in France, by a contemporary of Cuvier's, William Smith (1769–1839). Smith was a land drainer, mineral surveyor, and canal engineer who lived in and around Bath in the west of England for much of his life. As early as 1796 Smith had realized that fossils could be used to identify strata more securely than lithology (Fig. 4). He used this discovery to construct a table of strata

together with a sketch geological map of England and Wales in 1799, although only in 1815 was his great geological map published (Eyles *in* Schneer 1969). His methods became widely known in England through the writings of John Farey, Joseph Townsend, and particularly James Parkinson (1755–1824).

Parkinson was a London physician and one of the founders of the Geological Society in 1807. This Society was largely chemical and mineralogical in its earliest years, but rapidly took up stratigraphic studies using fossils until, by the mid-eighteenth-twenties, this was almost its exclusive concern. These studies, by men such as Thomas Webster, William Conybeare, and Gideon Mantell, were useful contributions to the steadily growing store of regional geological knowledge, which almost incidentally provided descriptions of previously unknown fossils. With the work of Murchison in Wales and the Welsh Borders in the eighteen-thirties, a whole new invertebrate fauna was brought into view. The Geological Society eventually took over

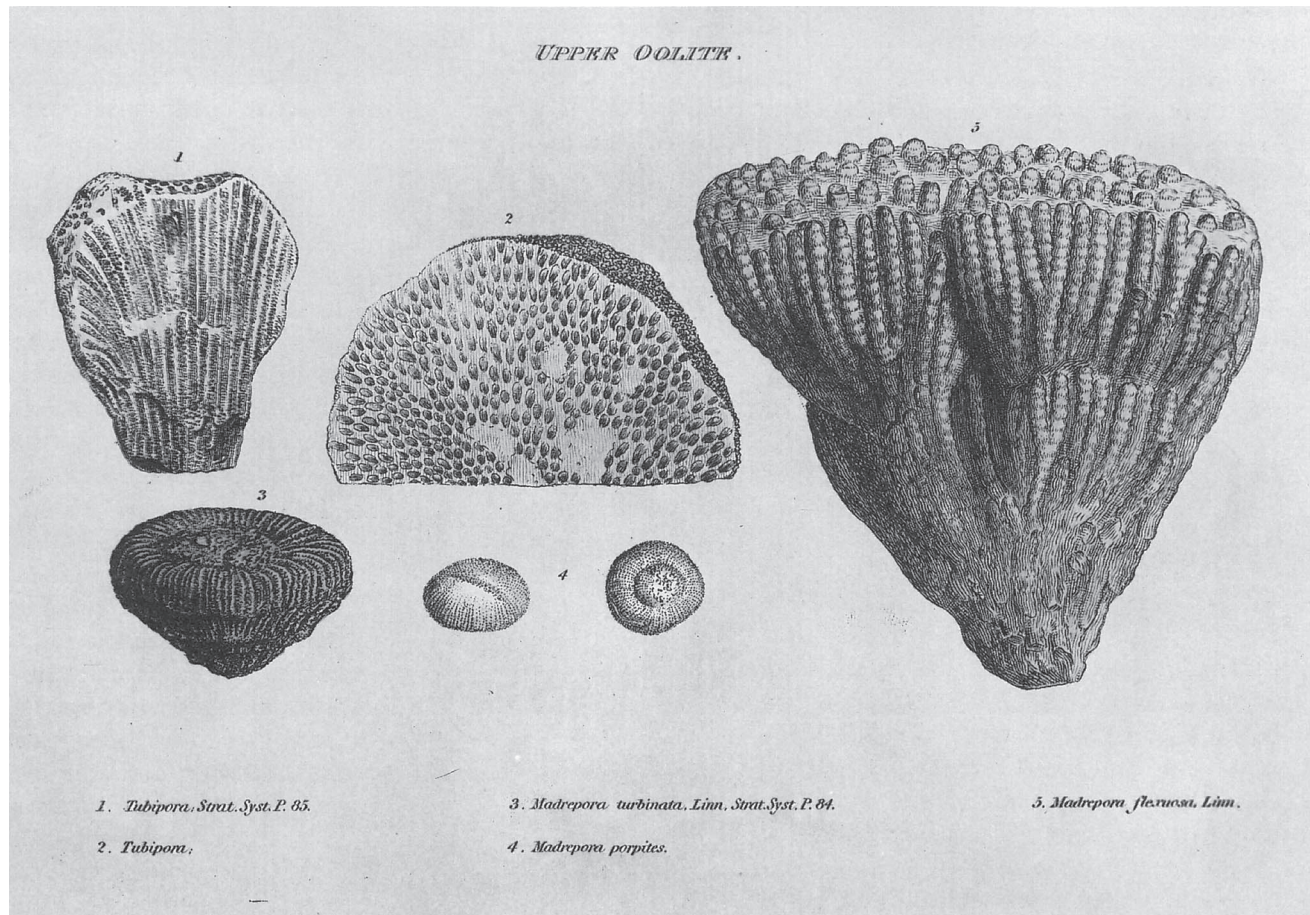


Fig. 4 Fossils of the Upper Oolite illustrated by William Smith in *Strata Identified by Organized Fossils* (1819, opposite p. 29).

from the Museum in Paris as the principal forum for palaeontological debate.

Although William Smith was hailed as 'the father of English geology', the influence of Cuvier was also very strong. His ideas on the relationship of fossils to Earth history came to England through the translation of his *Preliminary Discourse* by Robert Jameson (1774–1854). The book was entitled *Theory of the Earth*, which linked it in people's minds with the earlier theories of Woodward and Ray. In his notes Jameson tied Cuvier's chronology to the Bible in a way that its author had never done. He identified Cuvier's final revolution with Noah's Flood, and emphasized the dramatic and destructive power of the events. In doing this he reflected the characteristic theological slant of much British geology of this period.

The leading exponent of the Deluge in Britain was William Buckland (1784–1856), Professor of Geology and Mineralogy at the University of Oxford (Fig. 5). Although his main lines of evidence concerned erratic blocks and the shape of valleys, he was strongly influenced by the researches he carried out on bone caves in Yorkshire and elsewhere. Kirkdale Cave was discovered in 1821 and interpreted by Buckland, after careful study of the living animals, as the den of hyenas, whose long occupancy was ended by the Deluge. Along with this emphasis on Biblical chronology came a belief that the Earth and everything in it was designed for man. Buckland viewed the history of life within this tradition in his *Bridgewater Treatise* (1836), putting forward not only the sort of progression that Brongniart had advocated but also the idea that God had a guiding hand in adapting life in the best possible way to changing conditions (Rupke 1983, Ch. 2).

It is a salutary reminder of the state of palaeontological knowledge in the eighteen-thirties that another distinguished geologist and a pupil of Buckland, Charles Lyell (1797–1875), could argue that there was no sign of progression in the fossil record. He appealed, like Darwin later, to the poverty of collections and the lack of knowledge of many parts of the world, to show that negative evidence was no evidence. He made much of the discovery of mammals in the Oolitic rocks and of a reptile in the Devonian. He denied that early fossil fish, such as those found by Hugh Miller in Scotland, were any 'lower' than modern forms. This argument was used to back up his view that there was no evidence for the range of life, climate, environments, and geological processes ever being any different from those of the present day. Lyell also believed

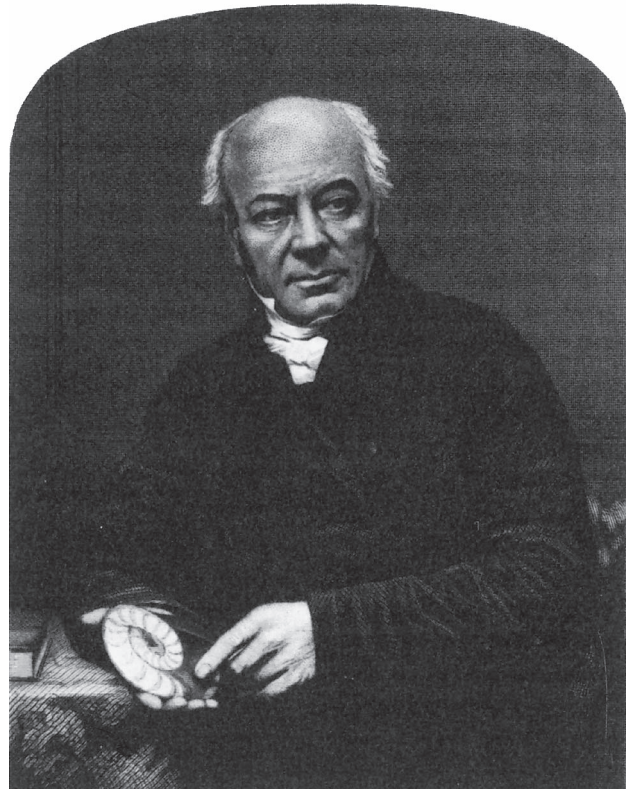


Fig. 5 Portrait of William Buckland published as the frontispiece to his *Bridgewater Treatise, Geology and Mineralogy*, 3rd edn (1858).

that personal religious belief must be kept quite separate from the study of fossils or any other aspect of geology (Bartholomew 1976).

Many features of Lyell's geology appealed to Charles Darwin (1809–1882). He read Lyell's *Principles of Geology* (1830–1833) while on the *Beagle*, and found it an excellent basis for interpreting the features he saw on his voyage. Lyell befriended him on his return and gave Darwin entrée to the Geological Society, where he met the experts he needed to work on his collections. Darwin's later writings on evolution, which were to influence all subsequent work on fossils, were not based on the study of the fossil record. In 1859 he was able, just like Lyell in 1830, to blame the inadequacy of the fossil record for not providing evidence to back up his theory.

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6.5.2 Darwin to Plate Tectonics

P. J. BOWLER

Introduction

Fossil discoveries continued apace in the late nineteenth century, but the theoretical foundations of palaeontology were transformed by the advent of evolutionism. For several decades the attempt to reconstruct the development of life on Earth using fossil and other evidence was the most active area of evolutionary biology, although this programme encouraged a distinctly non-Darwinian view of how the process worked. In the twentieth century palaeontologists somewhat belatedly adapted to the synthesis of Darwinism and genetics, and began to grapple more actively with the geographical dimension — although for many years they opposed the theory of continental drift.

New discoveries, 1860–1940

The impetus given to fossil collecting in the early nineteenth century was sustained in later decades by more extensive mining activities and by the opening up of new areas of the Earth to scientific exploration. In Europe and America major new

museums were founded to exhibit and interpret the discoveries to the public and as centres of research. The British Museum (Natural History) in London and the American Museum of Natural History in New York are obvious examples of museums that built up their reputations at this time. By the early twentieth century many large cities had similar institutions, giving rise to considerable rivalry in the establishment of good collections. Many of the new discoveries helped to fill in the outline of the history of life created by Cuvier and his followers, greatly extending knowledge of the dinosaurs and other groups which had originally been established on the basis of small numbers of incomplete specimens. The popularity of evolution theory focused particular attention on fossils that could be identified as 'missing links', again fuelling the rivalries of collectors and institutions.

The Miocene fauna of Pikermi, Greece, was studied by Albert Gaudry in the eighteen-sixties. His work threw new light on the proboscidean *Deinotherium* and on many other forms, leading Gaudry to support the concept of a continuous evolutionary development linking the known Eocene and Pleistocene faunas (Rudwick 1976; Buffetaut 1987). The discovery of an *Archaeopteryx* specimen with feathers at Solnhofen, Bavaria, in 1861 aroused intense excitement, especially after it was acquired (at vast expense) by the British Museum (Natural History) and subsequently described by T.H. Huxley as an intermediate between reptiles and birds. A second specimen was discovered in 1877. The unearthing of almost complete *Iguanodon* specimens at Bernissart, Belgium, in 1878 showed that these dinosaurs were bipedal, not quadrupedal as originally reconstructed (Colbert 1971). A mounted specimen in Brussels gave a new awareness of the appearance of dinosaurs from 1883 onwards. Other important collections of fossil reptiles came from the Jurassic Oxford Clay of Peterborough in Cambridgeshire and from Transylvania, the latter studied by the colourful and eccentric baron Franz Nopsca.

In North America, the opening up of the West led to a veritable 'war' between collectors such as O.C. Marsh and E.D. Cope. Their discoveries of Jurassic dinosaurs from Colorado in the eighteen-seventies greatly extended knowledge of the 'Age of Reptiles' and formed the basis of impressive museum displays. Marsh's discovery of toothed birds in Kansas supported the evolutionary link already suggested by *Archaeopteryx* (Fig. 1). Marsh also collected a series of fossils in Nebraska throwing light on the

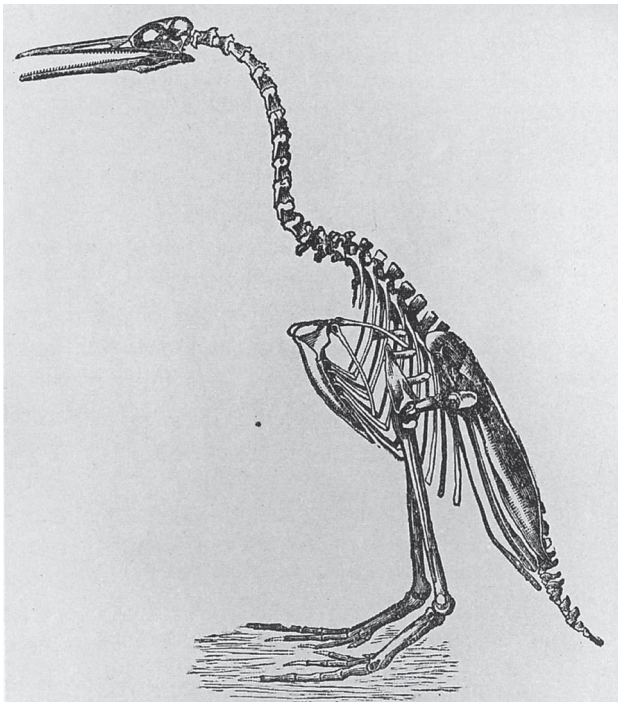


Fig. 1 *Hesperornis regalis* (Marsh). (From Huxley, T.H. 1888. *American addresses*. Appleton, New York, p. 52.)

evolution of the modern horse, culminating with the four-toed '*Eohippus*' in 1876. The fossil sequence was described as 'demonstrative evidence of evolution' by T.H. Huxley (Fig. 2). In the early twentieth century, H.F. Osborn described gigantic early mammals from the American west, including the titanotheres.

Of particular interest to the public were fossils relating to the origin of mankind (Reader 1981). In 1857 the discovery of a cranium at Neanderthal in Germany aroused much controversy but was eventually accepted as an early human form with some ape-like characters (Fig. 3). For some time considered as a possible ancestor of modern humans, the neanderthals were reinterpreted in the early twentieth century by Marcellin Boule, Arthur Keith, and others as a parallel and distinct human family driven to extinction by our own forebears. Eugene Dubois' discovery of '*Pithecanthropus erectus*' (now *Homo erectus*) in Java during the eighteen-nineties revealed an even earlier human form, again dismissed by many as a side-branch of our family tree. Thinking on human origins was to some extent thrown off course by the notorious Piltdown fraud of 1912, in which a human cranium and an ape jaw were attributed to an intermediate '*Eoanthropus*'. This reinforced the generally popular assumption

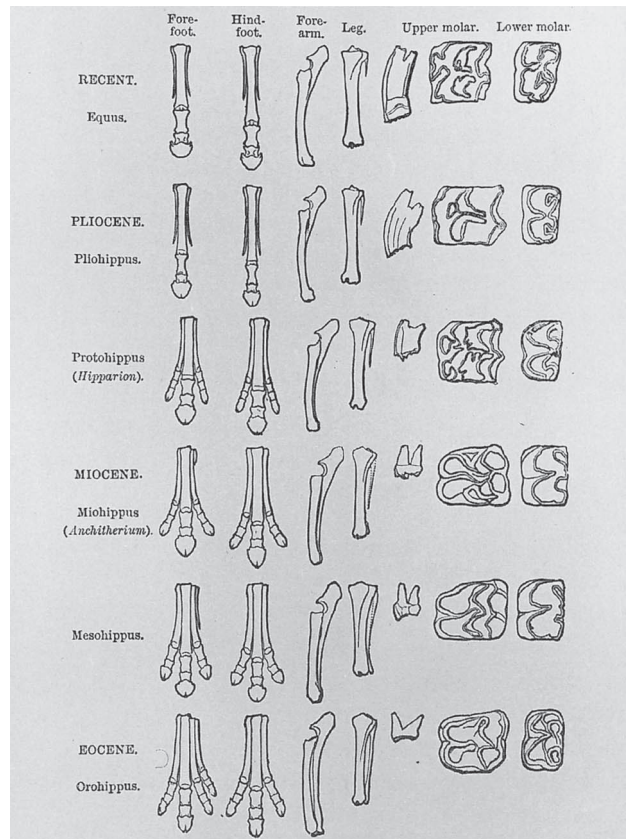


Fig. 2 Modification of the teeth and lower limbs of the horse family, after Marsh. (From Wallace, A.R. 1889. *Darwinism*. Macmillan, London, p. 388).

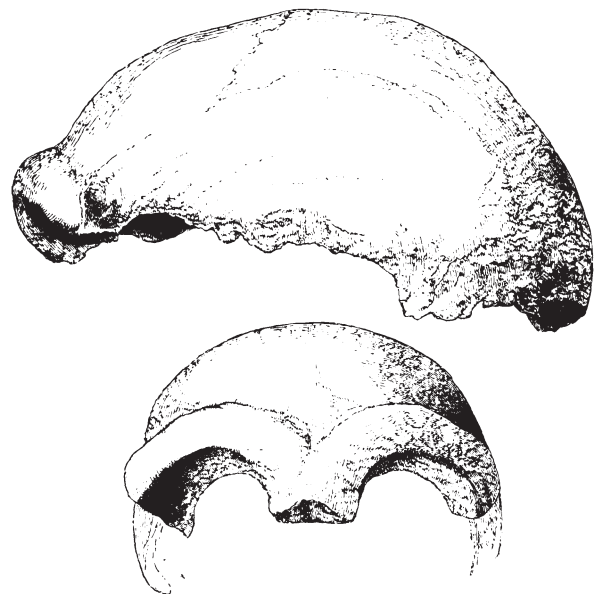


Fig. 3 The neanderthal cranium. (From Huxley, T.H. 1863. *Man's place in Nature*. Williams and Norgate, London, p. 139.)

that the expansion of the brain was the chief driving force of human evolution, making it easier to dismiss *Pithecanthropus*, with its small brain and upright posture, as irrelevant. Raymond Dart's discovery of the first australopithecine at Taung, South Africa, in 1924 was again dismissed because of the refusal to admit that a small-brained hominid could have achieved bipedalism. Dart was also ignored because of the widespread opinion that mankind must have evolved in central Asia, not Africa (although expeditions to Asia did reveal more *Homo erectus* specimens, at first known as *Sinanthropus* or Peking man). The australopithecines only began to be taken seriously after Robert Broom's discoveries of the nineteen-thirties.

Palaeontology and evolution theory

The search for 'missing links' ensured that evolutionism gave an added zest to fossil hunting, but it would be a mistake to overemphasize the impact of Darwin's theory on palaeontology. The description of fossils was still seen as a branch of morphology, with little attention being paid to intraspecific variation or the possibility of local effects on populations. Palaeontologists were thus not in the best position to appreciate the most original aspects of Darwin's theory. They had, in any case, begun to look for patterns of development in the fossil record long before the *Origin of species* appeared in 1859. The element of discontinuous change stressed by early catastrophists had begun to decline in the eighteen-fifties. H.G. Bronn and Richard Owen had begun to emphasize that there were 'laws of development' to be seen linking the fossils within each class, while the general idea of progressive evolution had been circulated as early as 1844 by Robert Chambers in his popular and controversial *Vestiges of the natural history of Creation* (Bowler 1976). It was recognized that the development of life included branching and what is now called adaptive radiation, but there was a preference for depicting the 'tree of life' with a central trunk leading through to the human race as the pinnacle of creation. The debate sparked off by Darwin's *Origin* certainly catalysed the scientific community's conversion to evolutionism, but the impetus for most palaeontological evolutionism came from transformations within the 'developmental' view of life's history already taking shape in the pre-Darwinian era. A few important figures, of whom J.W. Dawson of Montreal is the best example, continued to promote a discontinuous and hence anti-evolutionary view of

the fossil record. But in general the acceptance of a loosely-defined evolutionism came naturally to most palaeontologists, for whom the new approach was little more than an extension of the earlier search for abstract laws of development.

Many evolutionists saw their principal task as the reconstruction of the history of life on Earth using the fossil record, supplemented by evidence from comparative anatomy and embryology. In Germany, Ernst Haeckel popularized this version of 'Darwinism' in books such as his *History of Creation* (1876). Even T.H. Huxley only began to make active use of evolutionism in the study of fossils after reading Haeckel — his original support for Darwin was purely tactical (Desmond 1982). Palaeontologists now began to arrange the known specimens of each group into the most plausible evolutionary series, and of course to look for the missing links. Haeckel's recapitulation theory — the claim that ontogeny recapitulates phylogeny — was widely accepted by palaeontologists looking for clues as to the 'shape' of the pattern they should expect to find. In these circumstances, it is hardly surprising that many of their views on the mechanism of evolution were distinctly non-Darwinian in character. Haeckel himself was a Lamarckian, recognizing that the inheritance of acquired characters provided a better theoretical basis for recapitulation than natural selection. Many so-called 'Darwinists' might be better called pseudo-Darwinists, since their commitment was to evolutionism rather than to natural selection. In the later nineteenth century many palaeontologists became actively opposed to the selection theory (Bowler 1983, 1986). In America, an active school of neo-Lamarckism flourished from the eighteen-seventies onwards, led by the vertebrate palaeontologist E.D. Cope and the invertebrate palaeontologist Alpheus Hyatt. They too supported recapitulation and claimed that evolution occurred by regular extensions to the process of individual growth. Arrangements of fossils into apparently linear sequences, as in the case of the horse family (Fig. 2) helped to create an impression that evolution was too regular a process to be explained in terms of random variation and selection.

The fascination with 'laws of development' led many biologists to reject Darwin's claim that adaptation was the chief guiding force of evolution. They believed that factors internal to the organism would drive variation in a particular direction whatever the demands of the environment. On this model, one could expect parallel lines of evolution to advance steadily in the same direction over vast

periods of time. In Britain such a view was expounded by Owen's disciple St. George Mivart, who became one of Darwin's most active critics. Nor were Owen and Mivart mere speculators, since they recognized the possibility of mammal-like reptiles ahead of Huxley. Many palaeontologists supported the concept of *orthogenesis* (parallel evolution) driven by internal forces. Hyatt's arrangements of fossil cephalopods were widely accepted as classic examples of nonadaptive evolution. Vertebrate palaeontologists thought that many extinct species had developed grossly maladaptive characters before finally succumbing, one example being the antlers of the 'Irish elk'. Such ideas were still being promoted through into the nineteen-thirties by eminent palaeontologists such as H.F. Osborn. Osborn's subordinates at the American Museum of Natural History — including W.D. Matthew and W.K. Gregory — tried to sustain less extreme anti-Darwinian positions, but were still in a minority.

It would be easy to dismiss the palaeontologists' support for non-Darwinian concepts such as recapitulation, Lamarckism, and orthogenesis, as an aberration in the history of evolutionism, but this is a misconception engendered by our modern preference for the selection theory. In the late nineteenth century, non-Darwinian palaeontologists were in the forefront of evolutionary research, and they helped to shape the popular conception of what

evolutionism is all about. Their views were instrumental in circumventing the application of Darwinian principles to human origins: no one thought of specifying an adaptive scenario to explain why humans separated from apes, since it was assumed that the primates were governed by an inherent trend toward brain-growth. The popularity of parallel evolution helped to ensure that many hominid fossils were dismissed as the products of independent lines of evolution unconnected with our own origins. Such views remained acceptable to palaeontologists and palaeoanthropologists well into the twentieth century, long after they had been overtaken by changing attitudes elsewhere in biology (Bowler 1986).

The emergence of genetics at the turn of the century ensured that most experimental biologists soon came to repudiate Lamarckism, but palaeontology remained a morphological discipline and resisted the new trends. The 'Mendelian revolution' would eventually complete what Darwin had been unable to achieve: the destruction of the developmental world view characteristic of nineteenth-century morphology. But not until the nineteen-forties did palaeontologists begin seriously to take note of the new developments. It was G.G. Simpson's *Tempo and mode in evolution* of 1944 that forced the discipline to confront what has become known as the modern synthetic theory of evolution. The re-

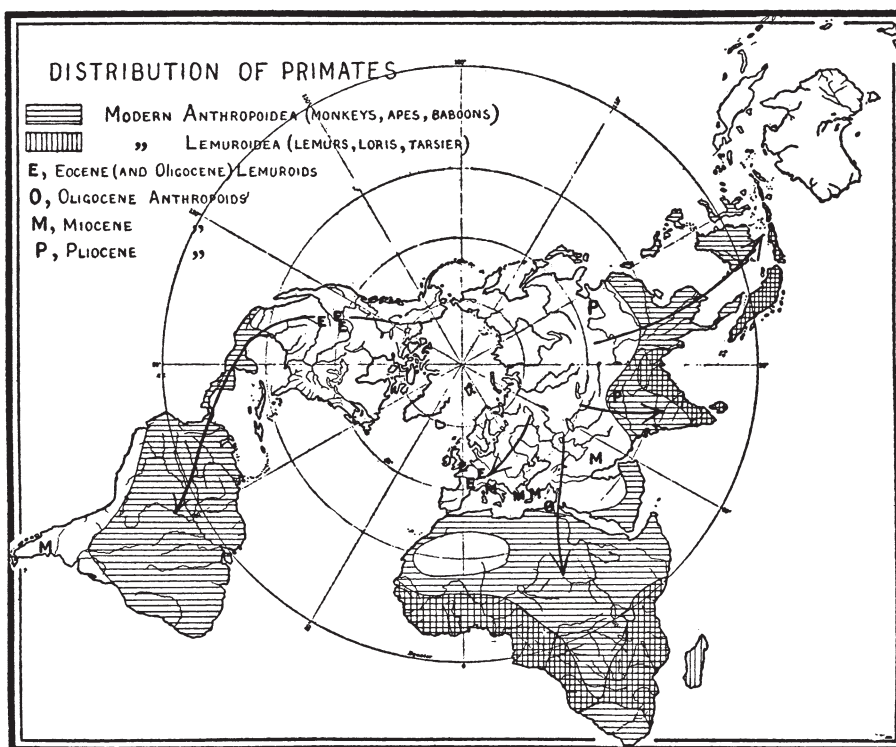


Fig. 4 Dispersal of the primates. (From Matthew, W.D. 1939. *Climate and evolution*. New York Academy of Sciences, p. 46.)

sult was a transformation in the kind of questions studied by palaeontologists in the postwar era. Parallelism and orthogenesis were replaced by adaptive scenarios and a greater concern for microevolution in local populations.

Palaeontology and geography

Although nineteenth-century palaeontologists were chiefly concerned with the creation of patterns of evolutionary development, their increasing knowledge of the world-wide distribution of fossils forced them to grapple with the geographical perspective. Darwin's theory drew attention to the apparently anomalous distribution of some modern forms and explained the phenomenon as the result of migrations in earlier geological epochs. Biogeographers postulated 'land bridges' in the past joining various parts of the Earth's surface. Palaeontologists also began to make use of this concept – Haeckel, for instance, suggested that the lack of fossil hominids could be explained by assuming that our ancestors had lived on the lost continent of Lemuria, now sunk in the Indian Ocean. When it was recognized that the Palaeozoic faunas of South America and South Africa were identical, it was natural to postulate a land bridge across the Atlantic which had sunk in the Mesozoic to allow the two continents' faunas to diverge. In thus ignoring the possibility of continental movement, palaeontologists merely followed the lead given by physical geologists.

Thinking on the geographical distribution of life in the Tertiary was deeply influenced by the Canadian-American palaeontologist W.D. Matthew, whose *Climate and evolution* of 1914 took the permanence of the existing continents for granted. Matthew saw central Asia as the heartland of mammalian evolution, from which waves of successively higher forms spread out to the rest of the world (Fig. 4). This theory was even extended to human origins, generating a widespread reluctance to take the discovery of hominid fossils in Africa seriously. When the possibility of continental drift was proposed by Alfred Wegener and a handful of followers, palaeontologists were in the forefront of opposition during the nineteen-twenties and nineteen-thirties. Charles Schuchert, in particular, defended the traditional concept of land bridges. Even G.G. Simpson wrote actively against continental drift in the nineteen-forties. The advent of plate tectonics in the postwar years thus represented a second major theoretical revolution to which palae-

ontologists had to respond. Land bridges were abandoned and the continental movements postulated by geologists have become major features of our current explanations of the evolution and distribution of life on Earth.

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6.5.3 Plate Tectonics to Paleobiology

J. W. VALENTINE

Introduction

During the period 1960–1975, palaeontology underwent a vigorous and lasting expansion of concerns and goals. While some of the roots of this expansion lay in earlier times, the formalization of concepts and the definition of problems that have grown into major features of palaeontological research occurred during this period. From its inception as a science, palaeontology has drawn upon both geological and biological sciences, and its findings have been applied to problems in each of those fields. It is thus appropriate briefly to mention major trends and events in biology and geology that became of particular importance to palaeontology.

Trends in earth science

The period was dominated by the rise of the plate tectonic paradigm (for a short historical account see Hallam 1973). Scattered but inconclusive evidence that the continents had held different geographical relations in the past had been adduced over several decades, but in the nineteen-fifties palaeomagnetic studies provided strong support for this hypothesis. Then in the nineteen-sixties the basis of differential movements of crustal segments was clarified. Hess (1962) suggested that oceanic crust was generated at deep ocean ridges and consumed in trenches, and palaeomagnetic studies of the sea floor soon provided supporting evidence. There followed a flood of geophysical experiments and observations leading to the development of the theory of plate tectonics by the close of the nineteen-sixties. During this period also, the need was felt for direct exploration of the ocean floor, and in 1964 a major initiative was launched to take deep cores of that floor (Joint Oceanographic Institutions for Deep Earth Sampling – JOIDES). This project led to the establishment of the Deep Sea Drilling Program (DSDP), the Reports from which had reached volume 27 by the close of 1974. The results of the drilling programme supported the implications of the geophysical data. Continents, continental fragments, and islands had ridden with the moving sea floor plates in which they were embedded. By 1973 many features of the relative positions of major continental masses were well enough worked out for palaeogeographic maps that covered most of Phanerozoic time (Smith *et al.* in Hughes 1973) to be constructed.

Trends in life science

Developments that affected palaeontology included a great rise in interest in the ecological disciplines, fuelled in part by concern over man's impact on the environment. Field exploration and experimentation were enlarged and extended into ecosystems, such as the pelagic and deep-sea realms, which had been poorly known and indeed misunderstood. Studies were particularly intense on factors regulating the ecological and evolutionary controls affecting the demography and distribution of natural populations, and on the principles that regulate the stability and diversity of ecosystems. Evolutionary studies were much concerned with processes of genetic change within lineages, and with speciation (e.g. Mayr 1963; Dobzhansky 1970) and with the

significance of neutral mutations in evolution (see Kimura 1983); and a beginning was made in evolutionary aspects of development from a molecular perspective (Britten & Davidson 1971).

Early history of life

Palaeontology in 1960–1975 flourished in response to its own traditional concerns and at the same time was increasingly influenced by contemporary events in earth and life sciences. Among the outstanding examples of palaeontological research were those which illuminated the fossil record of Archaean and Proterozoic life and of the earlier metazoan radiations. During the nineteen-sixties it became generally appreciated that stromatolites dating from the Archaean were marine algal structures. In 1965 a microbiota of presumed prokaryotes was described from the Gunflint Iron Formation, about two billion years old, which began a series of studies that revealed a microbial record extending back well into the Archaean (Section 1.2). This led to important syntheses of the geological and palaeontological evidence of Precambrian environments. A major element in the resulting hypotheses was that biogenic oxygen levels, representing a balance between supply via photosynthesis and consumption via oxidation of iron and other reduced substances, had risen across a variety of critical concentrations during the Proterozoic to permit the evolution of increasingly complex and active organisms.

The appearance of soft-bodied metazoan fossils in Late Precambrian rocks in the Ediacara Hills, South Australia was confirmed and the fauna described. Faunas in Europe, Africa, Asia, and North America, some known earlier and some now described, were identified as being similar to the Ediacaran assemblage, and the concept of a Late Precambrian metazoan fauna spanning perhaps 100 million years became established (Section 1.3). At the same time, it was proposed that there was a fauna, consisting chiefly of small enigmatic fossils, many phosphatic, that followed Ediacaran time but preceded the appearance of trilobites and echinoderms in the Early Cambrian. Elements of this fauna had long been known, but its distinctive position became clarified through descriptions of late Precambrian–Cambrian sections in Siberia and by synthesis of this stratigraphic data with records from Europe (Sections 1.4, 5.2.5). Also during the late nineteen-sixties and early nineteen-seventies, the soft-bodied fauna of the Burgess Shale of British Columbia was recollected and opened to restudy

and re-evaluation; it proved to be far less clearly allied to living taxa than had been supposed (Section 3.11.2).

From these studies the early history of life began to be written; life extended billions of years back in time, presumably beginning in an essentially anoxic environment. A radiation of soft-bodied metazoans preceded Cambrian time (Section 1.3), but nevertheless the abrupt appearance of metazoan phyla during the Early Cambrian did not appear to be an artifact, but to represent a true evolutionary episode of singular magnitude, producing many novel body plans.

Systematics and biostratigraphy

Researches on mineralized skeletal fossil groups of the Phanerozoic continued apace, with noteworthy activity in early Palaeozoic echinoderms, Permian brachiopods, early fishes, and taxa involved in the reptile–mammal transition. The organization and revision of scattered systematic and stratigraphic data into multivolume treatises, begun in previous years, continued, and these data were subjected to a further level of summarization in reviews of geological ranges of taxa, with assessments of changing diversifications, extinctions, and standing diversity levels, especially those of higher taxa in terms of their familial representation (Harland *et al.* 1967). Critical reviews of the methodology and application of biostratigraphy signalled increasing rigour in this area. Practical advances in biostratigraphy included the major refinement of zonations of late Mesozoic and Cenozoic rocks arising from study of micro- and nannofossils recovered from DSDP cores.

Palaeoecology and palaeobiogeography

Against this background of intense activity along well established trends, palaeontological subdisciplines that were in their infancy grew into major fields. Palaeoecology (Section 4) and palaeobiogeography (Section 5.5) are outstanding examples. As both industrial and academic programmes were employing palaeoecologists, a stream of students trained in biological as well as geological sciences was attracted to palaeontology, and many of the students had ecological interests. Early work focused on environmental reconstructions, thus contributing to geological interpretations; there was, however, growing interest in population and community palaeoecology and biogeography. Fossil assem-

blages were increasingly appreciated as representing the remains of biotic communities, and their description in this light tended to bring them to life and to fill them with new interest. Accordingly the interpretation of palaeocommunities and their palaeoenvironmental contexts became a common research goal, and the burgeoning literature of population and community biology was co-opted to serve as the basis for many theoretical aspects of the fossil record (e.g. Shopf 1972; Valentine 1973). Trace fossils, reflecting as they do the activities of organisms, proved to be sensitive environmental indicators of special importance, for they commonly occur in sediments otherwise devoid of fossils, and ichnology grew into a thriving subdiscipline (Sections 4.11, 4.19.4, 4.19.5). Still another branch of palaeontology expanded with the study of nannofossils and microfossils from DSDP and other deep-sea cores. The cores yielded planktic forms from surface and near-surface waters and benthic forms from the deep-sea benthos. Subjected to palaeoecological, biogeographical and isotopic analyses, these fossils permitted reconstruction of ancient ocean climates, current systems, biological productivity, and other features which contributed to the rise of the discipline of palaeoceanography.

The advent of plate tectonic theory provided a basis for the reconstruction of palaeobiogeographies that resembled historical reality on a global scale more or less throughout the entire Phanerozoic. The result was startling. Biodistributional patterns that had been attributed to either dispersal across 'land bridges' and 'stepping stones' (e.g. to bridge the early Mesozoic Atlantic Ocean), or to narrow biogeographical barriers between distinctive faunas (e.g. to explain the juxtaposition of American and European-type assemblages in the Early Cambrian of Northeastern America), were suddenly clarified. The 'land bridges' as envisioned did not exist, but rather the continents themselves had been juxtaposed during the Early Mesozoic; and the Cambrian barrier had once been an ancient ocean, long since subducted (see also Section 5.12). In addition to solving biogeographical puzzles of this sort, palaeogeographical reconstructions implied that environmental conditions, marine and terrestrial alike, must have varied in response to plate tectonic processes. Islands, continental fragments, and entire continents had moved between climatic zones and had been variously aggregated and dispersed. Not only would the climates of mobile geographical elements change as they entered new latitudes, but the climates themselves, and the circulation patterns

of atmosphere and ocean, would be affected. Distributional and associational patterns in the fossil record could now be placed in environmental contexts by evidence independent of the fossils themselves, and palaeoecology could now be concerned not only with the interpretation of local assemblages, but also with their contexts in regional and global patterns (Hughes 1973). It became possible in principle not only to apply and test theoretical notions from population and community ecology to fossils, but to formulate and test theoretical principles from fossil evidence.

Evolutionary studies

The growing confidence in applications of fossil data to biological theory was also exemplified in evolutionary studies. The patterns of morphological change observed among fossils did not always meet the expectations of many evolutionary models, and Eldredge & Gould in Schopf (1972) proposed that morphological changes within evolving lineages were concentrated at morphospeciation events, and that between such events change was slight — an alternation of morphological change and stasis that they termed 'punctuated equilibrium'. As these authors pointed out, long-term trends in morphological change could be attributed to the differential success of lineages that happen to exhibit change in a particular direction favoured by subsequent events, and need not indicate a history of phyletic evolutionary trends. Furthermore, the abrupt appearance of higher taxa in the record might indicate a punctuational origin. As for the fate of higher taxa, the accumulated data of their waxing and waning over Phanerozoic time led to studies of fossil taxonomic diversity (Section 5.3) and to theoretical models to account for their observed behaviours and for evolutionary change in general. In the Red Queen hypothesis (Section 2.5), for example, it was argued that adaptive improvement in a given lineage must perforce reduce adaptation in others, and when evolutionary processes acted to overcome this disadvantage, they produced adaptive deterioration in still other lineages; thus evolution must occur merely to maintain the status quo. From such hypotheses, the field of macroevolution was reborn within palaeontology.

As the concerns of palaeontology broadened, textbooks appeared that stressed these new interests (e.g. Raup & Stanley 1971) and new professional journals were established (*Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, from 1965; *Lethaia*, from

1968) that featured palaeobiological contributions. The journal *Paleobiology* appeared in 1975, marking the close of this period. During 1960–1975, palaeontology had become vastly enriched and diversified in a virtual 'evolutionary radiation' and within its many branches lay the potential for further fruitful expansion.

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6.5.4 The Past Decade and the Future

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Introduction

The scope of palaeontology is very broad, for it covers the entire history of life on Earth. Therefore, the spectrum of research strategies must also be very wide. During the nineteen-seventies, however, a gap appeared (and has continued to grow in the nineteen-eighties) between two major approaches to palaeontology. On the one hand, the traditional

approach — *palaeontology* — tends to emphasize the description of fossils and the reconstruction of extinct life as the basis for establishing a classification of organisms that reflects their phylogeny. The description of fossils and their distribution in the rocks is obviously important also for biostratigraphic correlation. On the other hand, many palaeontologists have boldly undertaken to search for general rules that may govern the causal process(es) responsible for the pattern of life, or the appearance and order of the biosphere. In this approach — which might be called *theoretical palaeobiology* — the empirical data of palaeontology are primarily employed for generating and testing theoretical hypotheses about the laws of organic and biotic evolution. The growing gap between palaeontology and theoretical palaeobiology has been the most conspicuous feature of the last decade in the history of palaeontology, but it must be closed in the future.

Palaeontology

That the palaeontographical approach is here regarded as traditional does not imply that such research is conducted today in the same way as it was in the last century, or even 20 years ago. New analytical tools have come into common use: electron microscopy, biogeochemistry, mineralogy, and even crystallography of fossils, etc. Incomparably more attention has been paid recently to the functional morphology of extinct organisms. The geological setting of fossils has also come more into focus, as recent developments in sedimentology allow quite detailed information about the habitat of extinct organisms to be deduced from the rock record. Palaeocommunity analysis has reached its peak as the means of describing the biotic environment of life forms in the geological past. In spite of such innovations and shifts in emphasis, however, the major achievements of this research strategy could conceivably have been made 20 years ago: discovery of the conodont animal, reinterpretation of many Ediacaran fossils, reconstruction of tabulates as sponges rather than corals, etc. Perhaps even more importantly, the main questions being asked within the conceptual framework of the palaeontographical approach have remained largely the same as before: What did extinct organisms look like, and how did they live? What is the shape of 'the tree of life' which links together the genealogies of all organic groups, both extinct and

extant? What was the ecological and biogeographical structure of the biosphere in the geological past?

To answer such questions using palaeontological data requires a methodology of historical reconstruction. This is the subject of the ongoing theoretical debates in palaeontology: the paradigm method of functional morphology versus constructional morphology in the reconstruction of organisms (Section 4.1), cladistic versus stratophenetic methods in the reconstruction of phylogeny (Section 5.2), etc. The rival methodologies refer also to contrasting perspectives on various problems in evolutionary biology: the relative roles of selection and constraint in phenotypic evolution (Sections 2.2, 2.3), the commonness of convergent and parallel evolution, etc. Thus, the palaeontographical approach to the history of life cannot be separated from theoretical considerations; yet within its conceptual framework, theory is not a goal in itself.

Theoretical palaeobiology

Just the opposite is the case with theoretical palaeobiology. In this approach, the emphasis is on the questions: Why is the shape of 'the tree of life' as it is? How does the process of evolution operate? What are the universal laws of organic and biotic evolution? The approach is therefore distinctively nomothetic. These questions are certainly not new; they were not posed for the first time in the nineteen-seventies. Palaeontology at an earlier peak (at the turn of the century and even well into the second quarter of the twentieth century) largely focused on these problems. Abel, Cope, Hyatt, Osborn, Wedekind, and Schindewolf all followed the nomothetic approach, regarding the fossil record primarily as the main source of empirical data relevant to these questions — at a time when the term *palaeobiology* was first coined. But the methodological rigour of modern theoretical palaeobiology, with its emphasis on pattern recognition and explanation through quantitative modelling and hypothesis testing, is entirely new. The beginnings of this research strategy can be traced back at least to Brinkmann (1929) but the onset of its explosive development is symbolically represented by the appearance of Schopf's *Models in paleobiology* (1972) and the founding of the journal *Paleobiology* in 1975. In retrospect, these publishing events seem to have been crucial in shaping the research area of theoretical palaeobiology.

Since about 1975, the research effort of theoretical palaeobiology has been primarily organized around

four subject areas of major controversy (for review and references see Hoffman 1988). In each case, the controversy chiefly concerned a proposal that some specifically macroevolutionary processes — irreducible to the microevolutionary processes envisaged by the neo-Darwinian paradigm of evolution — are responsible for the origin of the macroevolutionary patterns described by palaeobiologists.

1 Punctuated equilibrium. The concept of *punctuated equilibrium* seems to have attracted most attention, among palaeontologists as well as among other scientists and the general public. Perhaps the main cause for the heated debate on punctuated equilibrium has been the ambiguity of and repeated changes in the meaning of this concept since its original formulation by Eldredge & Gould *in* Schopf (1972). Its proponents and advocates have presented and argued for quite a number of substantially different versions (sometimes more than one within the body of a single article). In its 'weak' version, punctuated equilibrium is primarily meant as a contrast to so-called phyletic gradualism (i.e. the view that phenotypic evolution proceeds continuously in the same adaptive direction and at a constant rate). Punctuated equilibrium then means that the rate and direction of phenotypic evolution vary along a considerable proportion, or even an overwhelming majority, of phyletic lineages. When so understood, punctuated equilibrium is entirely trivial because this has never — since the advent of the neo-Darwinian paradigm — been seriously doubted by evolutionary biologists or palaeontologists.

The 'strong' version of punctuated equilibrium includes two assertions: (1) that phenotypic evolution never proceeds gradually, or that no significant evolutionary change is achieved by accumulation of small adaptive steps; and (2) that all phenotypic evolution is associated with speciation events. This latter assertion cannot be tested in the fossil record because, apart from a few instances of indisputable lineage splitting, speciation must be equated in palaeontology with considerable phenotypic change. The first assertion, however, has been repeatedly tested and refuted. In spite of a myriad of empirical problems, several cases of significant gradual evolution have been convincingly documented (Section 2.3). An even more radical variant of this 'strong' version of punctuated equilibrium is nevertheless tenable: that even an apparently continuous sequence of fossil populations may in fact consist of a discontinuous series of extinct species,

because continuity is always assumed rather than proven. This variant, however, explicitly enters the realm of metaphysics.

The 'moderate' version of punctuated equilibrium emphasizes the occurrence, and even commonness, of stasis in the evolutionary history of each phyletic lineage. When stasis is understood as the complete evolutionary stasis of the entire phenotype, this proposition is untestable because the fossil record provides data concerning only a small sample of anatomy while evolution may as well occur in soft-body anatomy, physiology, or behaviour. When stasis is understood to be the absence of change in some morphological characters, it certainly appears to be a widespread phenomenon. It may be due to a variety of microevolutionary processes, and it then perfectly fits the neo-Darwinian paradigm. To emphasize this phenomenon borders upon triviality. In principle, stasis may also be due to some constraints on morphological evolution which actively resist a change favoured by natural selection. The claim, however, that this is in fact the main mechanism of morphological stasis is unsupported by any evidence.

Thus, the debate on punctuated equilibrium has not led to the finding of any new evolutionary rules. It has, however, considerably raised the standards of palaeontological research on evolutionary rates and produced much fascinating empirical data on phenotypic evolutionary rates in a wide variety of fossil organisms.

2 Species selection. The results of the controversy on *species selection* are quite different. Since its first formulation (Stanley 1975) the concept of species selection has evolved as much as punctuated equilibrium, with which it was initially linked (Section 2.6). It is clear by now, however, that if species selection is meant to designate something more than just a net effect (on the supraspecific level) of natural selection at the individual level, then it must be defined as a causal process changing the relative speciosity of various clades due to selection for or against their heritable species-level properties. It also must be distinguished from species drift, i.e. the accidental change in species richness of various clades due to the vagaries of their environment or pure chance. Under such a definition, species selection is not related at all to punctuated equilibrium. It indeed represents a macroevolutionary process that can, potentially, operate in nature, but not one actual example of species selection has yet been convincingly documented. The debate on

species selection has thus resulted in expanding the scope of potential evolutionary forces which can, in theory, be invoked to explain macroevolutionary patterns, but the empirical research it stimulated has not been particularly productive.

3 Taxonomic diversification. Much palaeobiological discussion has been devoted to the problem of taxonomic diversification of the biosphere in the Phanerozoic. The very nature of the fossil record makes it difficult to establish the empirical pattern of change in global taxonomic diversity through geological time (Section 2.7). Assuming, however, that this pattern can be at least approximately represented by a global-scale compilation of the stratigraphic ranges of taxa at a supraspecific level, and at the time resolution of the geological stage, Sepkoski (1978) undertook a bold attempt at its causal explanation by a deterministic model. A variety of theoretical models have been subsequently proposed to account for these empirical data. Sepkoski's more complete equilibrium model of diversity-dependent diversification of three great evolutionary faunas which have displaced one another via biotic interactions seems to have attracted most attention (Section 1.6). However, a nonequilibrium model envisaging diversity-dependent diversification as driven by evolutionary novelties and mass extinctions may withstand the test of empirical data even better. These models explain the macroevolutionary pattern of taxonomic diversification in the Phanerozoic by reference to a set of specifically macroevolutionary rules, operating at a supraspecific level of biological organization. However, a simple stochastic model representing the pattern of taxonomic diversification as a net result of two independent random walks — one concerning the average rate of speciation, the other the average rate of species extinction per geological state — cannot be rejected as a null hypothesis. This model portrays the pattern of global taxonomic diversification as nothing but a by-product of a myriad of microevolutionary processes operating simultaneously upon a vast number of species in very many environments. Its apparent success, however, may also imply that the empirical pattern of diversity change through geological time is too heavily loaded by statistical noise to allow identification of the underlying causal process(es).

4 Mass extinctions. Perhaps the most spectacular debate in modern theoretical palaeobiology con-

cerns mass extinctions (Section 2.12). When taken in conjunction with the hypothesis that the Cretaceous–Tertiary mass extinction was caused by an extraterrestrial impact, the concepts of mass extinction periodicity (Raup & Sepkoski 1984) and biological distinctness from background extinction (Jablonski 1986) have led to the view that mass extinctions represent a separate class of macroevolutionary phenomena, caused by a separate category of macroevolutionary processes. Hence, a general theory of mass extinctions has been sought. Some palaeobiologists have even declared that this new perspective on mass extinctions refutes the neo-Darwinian paradigm of evolution. When considered in more detail, however, the components of this new perspective do not appear to be demonstrated beyond any reasonable doubt. The statistical test which was taken to indicate extinction periodicity seems to be biased toward this result. Moreover, a simple stochastic model is also capable of reproducing the empirical pattern of extinction peaks through time. Except perhaps for the Permian–Triassic crisis, the individual mass extinctions turn out to be clusters of events rather than single catastrophes, and there is no evidence to support the claim that they were all due to similar causes. Both hypotheses of an extraterrestrial causation of the Cretaceous–Tertiary boundary event and of a biological difference between the regimes of mass and background extinction are viable, but other rival hypotheses are at least equally plausible.

Thus, any attempt to develop a general theory of mass extinctions must be judged precarious. In terms of its theoretical consequences, the research on mass extinctions may therefore be regarded as fruitless, at least for the moment. On the other hand, it has been enormously productive in terms of empirical data, for it has stimulated much innovative work — palaeontological, microstratigraphical, sedimentological, geochemical, and mineralogical — at the stratigraphical horizons considered to represent times of mass extinction.

Other topics. These four major debates in theoretical palaeobiology of course do not cover the entire area of its research interests. Much consideration has also been given in the last decade to topics such as the evolutionary implications of the ecological organization of the biosphere. The laws of community evolution have been sought but thus far not found (Section 4.17), not only because the conceptual framework of community palaeoecology is at present too cloudy, but perhaps also because such laws

are rather unlikely to exist, as ecologists continue to remind palaeobiologists (Futuyma; Underwood; *both in* Raup & Jablonski 1986). Van Valen's (1973) Red Queen hypothesis has directed much palaeobiological research toward analysis of the significance of diffuse coevolution for evolution in ecosystems (Section 2.5). Thus far, however, the results are largely inconclusive (Hoffman & Kitchell 1984).

The future

In spite of considerable efforts undertaken within the framework of theoretical palaeobiology, no new biological laws, or even inductive generalizations, have been demonstrated by studies on the history of the biosphere. Perhaps there are no macro-evolutionary rules which could be detected by palaeobiologists; if so, the nomothetic approach of theoretical palaeobiology would be counterproductive — but, of course, we cannot possibly know whether or not this is indeed the case. Or perhaps the palaeontological data presently available for palaeobiological analyses are inadequate because they are collected entirely within the framework of palaeontography, for purposes other than testing general hypotheses about the process(es) of evolution. If so, a substantial improvement in the empirical database is badly needed — but such an improvement will only be possible when the gap between theoretical palaeobiology and palaeontography is closed.

In either instance, however, a change in emphasis for palaeontology appears to be inevitable. Palaeontology has become much more fascinating (and also fashionable) in the last decade than it used to be. It owes this success largely to theoretical palaeobiology, because in the eyes of many scientists and public alike the essence of science is to seek general laws. No wonder that palaeontography has often been looked upon as a rather dull, though admittedly necessary, companion of theoretical palaeobiology. Yet palaeontology is first and foremost a historical science. Palaeontologists are primarily historians of the biosphere and must focus on reconstructing history. The history of the biosphere, however, may not be shaped according to a set of general biological laws. Karl Popper's (1945) *Poverty of historicism* should long have been obligatory reading for palaeontologists. The emphasis of palaeontological research must shift back to the study of unique, historical biological events and chains of events; it must follow the idiographic approach.

Only then should we attempt to seek inductive generalizations about the evolution of lineages, the waxing and waning of clades, mass extinctions and explosive radiations of taxa, etc.

Research on particular events and sequences of events, however, should meet the new standards introduced to palaeontology during the last dozen years or so. Models of these phenomena should be developed and rigorously tested, quantitatively whenever possible. To this end, a detailed stratigraphic framework and a coherent taxonomic system are absolutely crucial. This is not only an empirical challenge but also a theoretical one; for while cladistics may provide a methodology for systematics, its application to taxa of variable geological age is not a simple matter, and the methodology of biostratigraphy seems to be rather undervalued and consequently underdeveloped.

Perhaps even more importantly, however, palaeontology must ultimately break down the barriers that have for long separated it from many other disciplines within the earth and life sciences. In the last decade, these barriers have already begun to collapse. On the one hand, palaeontologists are beginning to look to molecular and cell biology for a better understanding of fossil organisms (Section 2.1). This may lead to the demonstration that morphogenesis of the skeletal parts — which are the objects of palaeontological study — is under much stronger environmental controls than traditionally accepted. Were it so, the implications for palaeontological interpretation of fossil morphologies and their variation in space and time would be tremendous. On the other hand, palaeontologists are beginning to view the biosphere as a component of a global system which encompasses life, ocean, air, and the lithosphere. This trend is reflected by the growing interest among palaeontologists in stable isotope geochemistry, palaeoceanography, and palaeoclimatology (Section 4.19). The promise of these disciplines for the history of the biosphere lies in their potential to shed new light on the workings of the global system and hence, indirectly, on the state of the biosphere.

For the future of palaeontology, I thus envisage a more humble focus on reconstruction of the history of life, rather than on attempts to discover the laws of this history; but I also envisage a considerable expansion of the scope of palaeontology to include all aspects of the history of life on Earth, rather than solely the history of particular lineages, clades, or communities. To this end, however, we must always be very explicit about the biological entities we

undertake to describe and reconstruct — whether we talk of genotypes, phenotypes, or single traits, whether of phena, biological species, or phyletic lineages, whether of taphocoenoses, ecological communities, or taxocoenoses — and we must also be explicit about the limitations of our biological interpretations. Otherwise, palaeontology will inevitably fall back to the stage of mere story-telling.

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