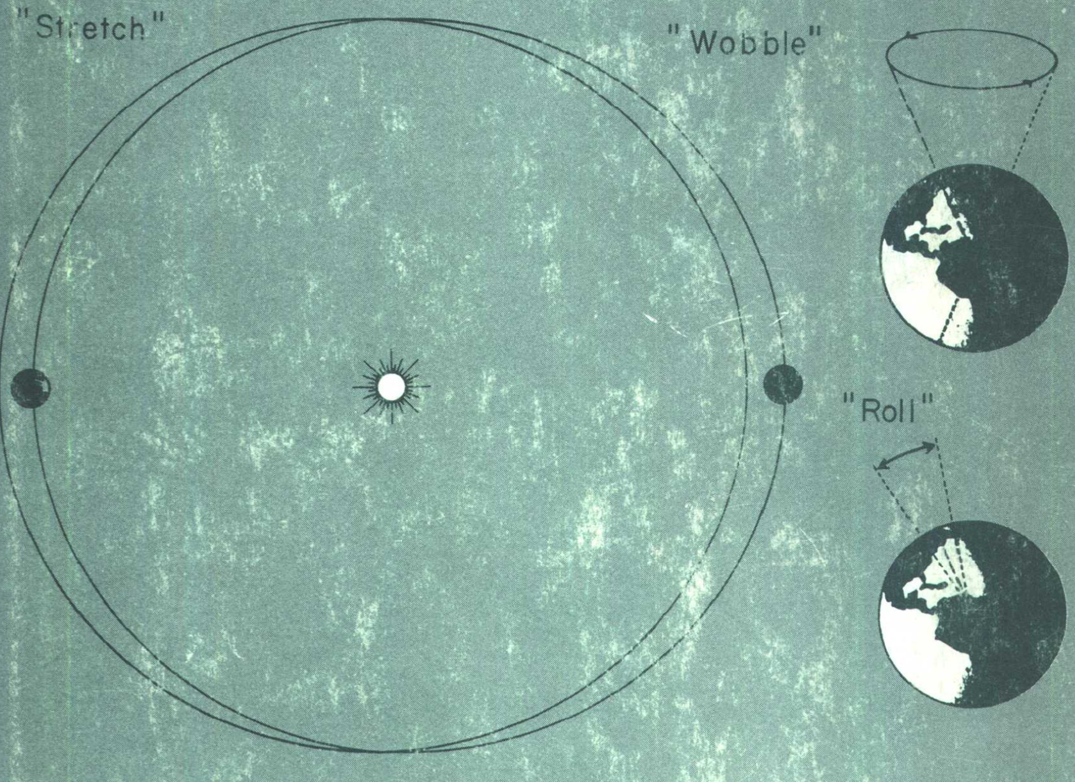
Climate and Evolution



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Preface

Climatic changes, whatever their causes, have far-reaching effects upon living organisms. It is such changes, and their probable effects during the last thousand million years, that are the subject of this book. Their involvement in biotic history can take three different forms. First of all they can affect the rate of evolution by varying the intensity of the selective pressures acting at given moments of world history. This, it is suggested, gave rise to the changing faunal and floral associations of geological time. Secondly, changing climatic conditions shaped the environments in which Man and all other species evolved, and in which present-day species achieved their distributions. Finally, and during the last few thousand years, continuing changes of a less extreme nature have exerted crucial influences on many important historical events.

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Introduction

1 GENERAL CONSIDERATIONS

The history of ideas includes many ironies. Concepts have frequently risen to prominence, or sunk into disrepute, along with the changing whims of fashion. Some ideas are speedily accepted and become widely influential from the moment of their formulation whilst others lack this initial phase of enthusiastic acceptance and remain decried, disputed, or simply unheard of, their existence known to relatively few people for long periods after their inception. Time and time again valid concepts have only been recognised as such long after their initial promulgation. Neither history guarantees the continued acceptance of such ideas despite evidence that they are correct. Indeed there seems to be a pronounced cycle. Ideas gain acceptance in one generation, become *passé*, and are then rediscovered, often independently of the early literature, by a later generation. It is difficult, indeed impossible, to point to any universal, common factor in such cases, apart from saying that the ideas are, at various times, unacceptable to certain arbiters of fashion. Retrospectively their history clearly says more about those arbiters, and the socio-political environment in which they lived, than about the ideas themselves.

One example that is particularly relevant to the subject matter of this book can be considered briefly here. Others, which relate to historical climatology, occur in subsequent chapters. At the time that "The Origin of Species by Natural Selection" was published many paleontologists still shared the view of Cuvier (1769–1832) and Alcide d'Orbigny (1802–1857) that the history of life on earth had been marked by a series of catastrophic extinctions. Actually the cataclysmic nature of natural processes was far from being peculiar to the theories of Cuvier and occurred elsewhere in the works of Lomonosov (1711–1765), Hutton (1726–1797), von Hoff

(1771–1837) and even Lyell (1797–1875). All such thinkers regarded floods, volcanic eruptions and earthquakes as natural phenomena that were just as relevant to the past as to the present; although Lyell emphasised the slow and uniform effects rather than episodic changes. Whilst he noted that the specific conclusions of such workers bear relatively little direct relationships to modern ideas, Newell (1967) pointed out that the "stratigraphic column" was certainly characterised by discontinuities of both lithology and fossil content. There is actually nothing in the fossil record to justify "catastrophism" as Cuvier himself understood it, nor, for that matter, a literal interpretation of Lyell's uniformity, but, nevertheless, in the early nineteenth century the known facts of paleontology seemed to justify the former. However, following the publication of Darwin and Wallace's ideas on evolution, considerations of episodic phenomena were largely abandoned by zoologists because it was considered that they conflicted with the tenets of natural selection. Indeed it was really only the publication of Umbgrove's book (1947) that led to long-term periodic phenomena, other than those relating to Quaternary climates, being considered by biologists again.

Many workers would, today, admit that there have certainly been some four or five critical environmental revolutions in the past (cf. Berkner and Marshall, 1964; Fairbridge, 1967; and Valentine, 1973). These may be listed as:

1. The appearance of the first living systems, *c.* $3{\cdot}8 \pm 0{\cdot}3 \times 10^9$ years B.P.
2. The appearance of the first photosynthetic systems, O_2, *c.* $2{\cdot}8 \pm 0{\cdot}2 \times 10^9$ years B.P.
3. The first carbonate shells, *c.* $6 \pm 0{\cdot}3 \times 10^8$ years B.P.
4. The great coal age, *c.* $3{\cdot}5 \pm 0{\cdot}3 \times 10^8$ year B.P.
5. The appearance of carbonate plankton, *c.* $1{\cdot}0 \pm 0{\cdot}2 \times 10^8$ years B.P.

During the period that has elapsed since the publication of Umbgrove's book a number of authors have also drawn attention, often quite independently, to other somewhat periodic aspects of world faunal and floral history. Clearly any change in environmental conditions affects a variety of taxa to a greater or lesser extent, but the principal problem with which such ideas are concerned relates to possible, contemporaneous, world-wide changes of the environment that have affected the existing biota and given the varying faunal and floral associations of the past. It is upon these that the classical divisions of geological time are based. Complementary and related problems refer to periods of geological time within which there appear to have been widespread extinctions.

Simpson (1952), considering the vertebrate record, concluded that episodes of "explosive evolution" cannot be defined as limited to, or caused at, any particular point in time. In particular, it was not, in his opinion, possible to demonstrate a causal relationship between such supposed episodes of extinction and periodic, diastrophic periods affecting the earth's crust. However, in the same symposium, Newell (1952, see Fig. 1) drew contrasting conclusions when he considered

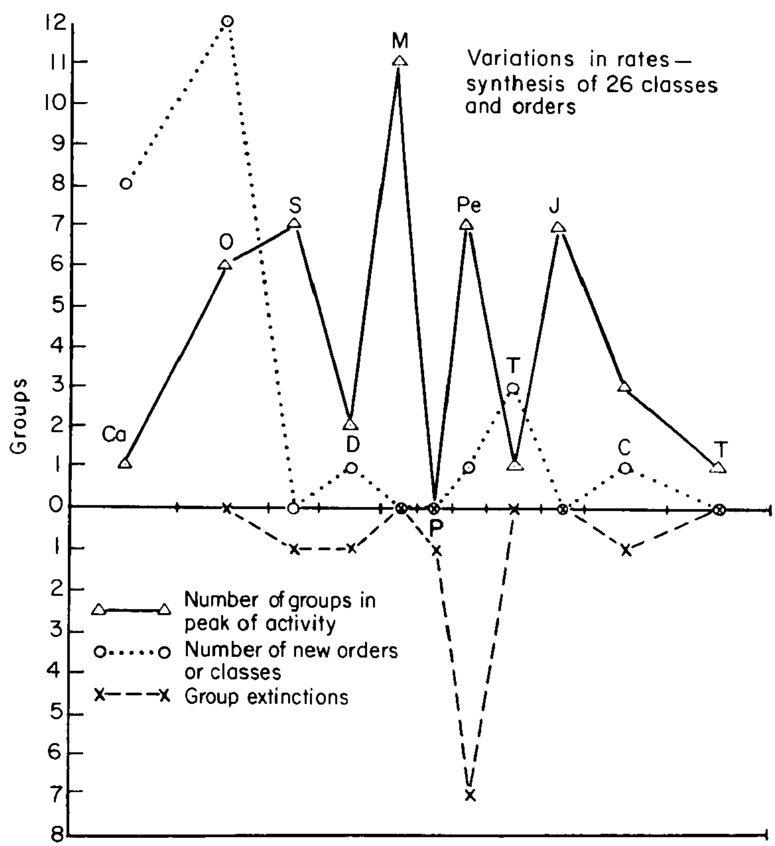

FIG. 1. A synthetic graph showing the times at which there appear to have been the highest rates of generic differentiation, together with the suggested times of the first appearance and the disappearance of the major taxa of invertebrates (Newell, 1952). Ca, Cambrian; O, Ordovician; S, Silurian; D, Devonian; M, Mississippian; P, Pennsylvanian; Pe, Permian; T, Triassic; J, Jurassic; C, Cretaceous; T, Tertiary. Compare Figs 46 and 49.

the invertebrate succession. He favoured climatic explanations for such periods of extinction and these were subsequently proffered, often independently and alongside periodic orogenic activity, by van der Hammen (1961), Pearson (1964), Ager (1973) and Budyko (1974). Such explanations envisage periodic or sporadic climatic changes as the "cosmic clutch" that has varied the pace of evolution by changing the intensity and precise nature of the selective processes acting at given moments of world history. Emergent data on geophysics and climatology now go a long way towards supporting such suggestions.

Although various suggestions which involve other parameters have been proposed, the discovery of geomagnetic reversals, and their association with climatic changes, has now focussed attention on this basic thesis. Complementarily, our knowledge of plate tectonics, which demands differing geographies in the past, as postulated by Köppen and Wegener (1924), necessarily implies changing environmental and climatic régimes.

2 THE PHANEROZOIC TIME SCALE

Relative time scales for geological events were established in the last century by the use of stratigraphy and paleontology. Those sequences which existed in particular localities were correlated on an international basis by comparing the type fossils, and components of faunal assemblages. Although the initial values that were given for the various ages on this basis now seem hilarious it is essential to view them in the context of the historical, and, more particularly, the biblical background of the times. Such age determinations undoubtedly had a great influence upon contemporary conclusions about evolution. In 1893 Walcott proposed that the Paleozoic had lasted some 17½ m.y. (million years), the Mesozoic 7 m.y., and the Cenozoic 3 m.y. Around the same time Lord Kelvin suggested that a minimum of 20 m.y., and a maximum of 400 m.y., had elapsed since the earth was molten. These figures were subsequently corrected by Goodchild, in 1897, who concluded that 704 m.y. had elapsed since the beginning of the Cambrian.

It was only with the advent of modern, radiometric methods of age determination that it became possible to establish an independent absolute chronology with any degree of certainty and an interesting review of the early attempts at age determination is provided by Wager (1964). Reviews of more modern work are provided by Holmes (1959), Faul (1960), Kulp (1961), Evernden and Richards

(1962) and York and Farquhar (1972). The most comprehensive analysis is provided by the symposium volume (1964) of the Geological Society of London.

In principle the easiest method of assigning dates to given periods is to collect fossiliferous material from their initial and final phases and apply to it the radiometric techniques that are currently available. In practice this is not an easy process, because of the great difficulty experienced in obtaining reliable dates from sediments, and two other approaches have therefore been favoured. These comprise dating volcanic rocks that are interbedded between sediments of proven stratigraphic position, or dating igneous intrusives that have been obtained under comparable circumstances. Volcanic rocks can be dated in a number of ways which are broadly dependent upon their composition. Minerals such as sanidine, biotite, plagioclase, and whole rock basalts are exposed to the K–Ar or, occasionally, the Rb–Sr techniques. The dating of igneous intrusives is usually accomplished by Rb–Sr whole rock analysis coupled with the analysis of component minerals by the Rb–Sr and K–Ar techniques. However, a hazard of such approaches lies in the fact that plutonic bodies may have spent a considerable time at depth during which time they lost daughter isotopes and therefore give a wrong value. Complementarily, intrusives are frequently difficult to place in their correct stratigraphic position and are therefore less reliably ascribed than the lavas noted above.

For these and other reasons the various values included in the *QJGS time scale* are of varying validity. For example, McCartney *et al.* (1966) concluded that 560 ± 11 m.y. was reasonable for the base of the Cambrian but York and Farquhar (1972) favoured 590 m.y. It was, however, the Silurian which had the worst radiometric coverage of all and the QJGS values were modified by the last-named authors. Their conclusions on these and other periods are summarised in Table 1.

3 BRIEF HISTORY OF THE CONCEPT OF EVOLUTION

In general terms Linnaeus epitomised the view that all species are fixed and immutable, and declared in his "Fundamenta Botanica" (1736) that nature "has as many species as were created in the beginning". Nevertheless, prior to Linnaeus and Ray it was widely thought that any species could give rise to practically any other one, so that, far from being an obstacle to scientific progress, the views of Linnaeus introduced some order where confusion had previously

TABLE 1

The Phanerozoic time scale (after the QJGS, 1964, and York and Farquhar, 1972)

	m.y.		m.y.
CENOZOIC		PALAEOZOIC	
Quaternary		*Permian*	
Pleistocene	1·5–2??	Upper	240
Tertiary		Lower	280
Pliocene	*c.* 7	*Carboniferous*	
Miocene	26	Upper	325
Oligocene	37–38	Lower	345??
Eocene	53–54	*Devonian*	
Palaeocene	65	Upper	359
MESOZOIC		Middle	370
Cretaceous		Lower	395?
Upper	100	*Silurian*	430–440???
Lower	136?	*Ordovician*	
Jurassic		Upper	445?
Upper	162	Lower	*c.* 500?
Middle	172	*Cambrian*	
Lower	190–195	Upper	515?
Triassic		Middle	540?
Upper	205	Lower	570?
Middle	215		
Lower	225		

reigned, and the known occurrence of hybrids etc., forced even these concepts to remain open to some discussion. Adanson in his "Histoire des Familles des Plantes" (1763) argued against the absolute fixity of species, conceiving that transformations were related to the action of such external factors as domestication and climate. Buffon, who devoted much of his time to the problem of species, and tried to cross dogs with wolves, rabbits with hares, and goats with sheep, also came down in favour of limited variability, and expressed his "transformist" views most clearly in discussions of the "degeneration" of animals under the influence of climate and domestication.

Maupertuis was one of the first people to overtly accept and promulgate "transformist" ideas, and his "Essai sur la Formation des Corps Organisés" (1754) is a fairly definitive landmark in natural history. An analogous contribution of great importance was the

"Zoonomia, or the Laws of Organic Life" by Erasmus Darwin (1794), which contained a theory of the gradual "transformation" and "perfection" of the animal kingdom. "Improvements" were here considered to result from responses to a variety of external stimuli such as climate, habitat, food, diseases and domestication. Apart from rather "Lamarckian" ideas about how the trunks of elephants enable them to feed on high branches, the Zoonomia included the beginnings of such Darwinian notions as protective coloration, sexual selection etc. Indeed, by this point at the close of the eighteenth century the new doctrine of "Transformism" was clearly fairly firmly entrenched.

It was at this time that Lamarck's position at the Natural History Museum in Paris, in which he was given the job of reclassifying the collections, led him to reject the belief in the immutability of animals and in his "Philosophie Zoologique" (1809) he propounded a theory of evolution. In this he concluded that new needs "create" new organs, with the degree of development of these organs being proportionate to the use made of them, and, perhaps more important in view of subsequent controversy, that everything which an individual acquires during the course of its life is preserved and transmitted to its descendants. He was supported by Sainte-Hilaire (1772–1844) but Cuvier was one of his most overt critics.

A large part of Cuvier's own scientific activity was directed towards paleontology. His first paper on the subject, in which he compared extinct and extant species of proboscideans, was followed by a series of similar studies that culminated in the first edition (1812) of his "Récherches sur les Ossemens Fossiles ou l'on Établit les Caractères de Plusieurs Animaux dont les Révolutions du Globe ont Détruit les Especes". A second edition embodying many new facts was published in 1821–1824, whilst a third edition (1825) only differed from the foregoing in a number of alterations to the "Preliminary Discourse" which was also published under the title "Discours sur les Révolutions de la Surface du Globe". According to Cuvier, three distinct faunas had inhabited the globe during three distinct epochs. The first included giant fishes and reptiles but only a few small mammals; the second, during which land mammals came to the fore, was represented by *Paleotherium* and *Anoplotherium*; whilst the third comprised the mammoths, mastodons, hippopotami and rhinoceroses. The methods he used were, at least in essence, those which are still used today, and even his precipitate denial of the existence of any intermediate forms evinced an extensive search for them which guided paleontology into its later channels. However, the conflict between his simplistic "catastrophism" and the complexity of the fossil deposits which were even then being described, resulted in his seminal idea bearing little relationship to the data of this book.

It is undoubtedly a truism to say that the reception given to new ideas changed between 1789 and the first decade of the nineteenth century. Received with enthusiasm in the later decades of the eighteenth century, they were later to be inextricably confused, in the minds of European literati, with the horrors of the "Terror". This appears to have had an influential and unfortunate effect on the ideas put forward in biology. It was, perhaps, the publication of Lamarck's thesis that led three physicians, Wells, Prichard and Lawrence, to independently repudiate the concept of the inheritance of acquired characters. Their views, which were published in the second decade of the nineteenth century, all advanced, in varying degrees, the alternative theory of natural selection which had been foreshadowed by the writings of Erasmus Darwin. However, it was not a propitious moment for the publication of such ideas. Lawrence's book "The Natural History of Man" argued that the differences which exist between the various races of man are hereditary, have arisen by such changes as one can observe amongst litters of rabbits or kittens, and are maintained by barriers against their interbreeding. He also considered that such changes were unrelated to direct effects of food, climate etc.; concluded that men could be improved or ruined by selective breeding, just as domestic animals could be; and drew a political moral by using the European royal families and aristocracies as examples. It was almost certainly this thesis that led to the legal withdrawal of the book immediately after its publication. His suggestion that the European royal families, together with corrupt and mentally deficient aristocrats, could be improved by applying the processes of stockbreeding, would have fallen on many receptive ears and the influential figures, horrified by the recent history of France, might reasonably have been expected to attempt to suppress it. Furthermore, his discussion of the orang-utan theory of man's origins, relieved by vivid references to the buttocks of Hottentot women and what he called the "rites of Venus", was eminently readable. As Darlington (1959) remarked, the clergy read it, probably enjoyed it, and denounced it. The laity read it and enjoyed it. From Lawrence they could learn the principle of sexual selection and the analogy with animal breeding which was later to be inextricably associated with, and ascribed to, Charles Darwin. Alongside this were discussions of mutation; a comparative study of skulls which