LIFE, TIME AND DARWIN

Inaugural lecture of the
Professor of Geology
delivered at the College
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LIFE, TIME, AND DARWIN

THIS year marks the centenary of one of the most important events in the history of science. At a meeting of the Linnean Society of London on 1 July 1858 Charles Darwin and Alfred Russell Wallace presented a joint paper entitled 'On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection'. The association of the two authors was remarkable. In February 1858 Wallace lay stricken with fever at Ternate, in the jungles of the Moluccas. As his mind wandered over the problem of the development of species, a subject that had exercised his attention for a number of years, he suddenly recalled an *Essay on Population* by Rev. Robert Malthus, which he had read twelve years before. Malthus argued that the human race would increase in a geometric progression were it not for the fact that many of its members failed to survive and to reproduce. 'In a sudden flash of insight' Wallace realized the applicability of this to the organic world as a whole and conceived the idea of natural selection in the development of species. Within a week he sent to Darwin a summary of his conclusions under the title 'On the Tendency of Varieties to depart indefinitely from the Original Type'. Wallace wrote that the idea expressed seemed to him to be new, and asked Darwin, if he also thought it new, to show it to Sir Charles Lyell.

Darwin received the essay with astonishment and dismay, for Wallace's hypothesis was identical with that which he himself had formulated. Darwin, who curiously enough had also been much influenced by Malthus's essay, had devoted the previous twenty years to the patient accumulation of evidence which he proposed to publish as a book. Year after year Darwin accumulated more and more data and slowly the enormous treatise took form, although he had, in fact, prepared an outline of his theory as far back as 1842, and a more lengthy account two years later. Of these, he wrote to Lyell, 'I never saw a more striking coincidence; if Wallace had my MS. sketch written out in 1842, he could not have made a better short abstract! Even his terms now stand as heads of my chapters'. It was under such circumstances that Sir Charles Lyell and Sir Joseph Hooker suggested a joint presentation of papers announcing the theory. Darwin and Wallace readily agreed, and the joint publication included Wallace's essay and an extract from Darwin's manuscript of 1844, together with an extract from one of his letters to Asa Grey written in October 1857 'in which (as Lyell and Hooker noted in their accompanying letter of presentation) he repeats his views, and which shows that these remained unaltered from 1839 to 1857'. The paper was calmly received and few of those who heard it could have predicted the way in which this new theory of evolution was soon to shatter the tranquillity of Victorian thought.

The following year Darwin completed a brief abstract (as he called it) of his researches and on 24 November 1859, there was published the most important book of the century—*The Origin of Species*. On the day of its publication the first edition of 1,250 copies was sold out.

The effect of *The Origin* upon public opinion was immediate and profound, but its effect upon the natural sciences was revolutionary. It provided the key that not only integrated and interpreted the maze of biological data but also gave new impetus and urgency to every avenue of research.

To Darwin, as to Wallace, the ultimate solution of the problem of the origin of species came suddenly, 'In

October 1838' he wrote '. . . I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on, from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. . . . I can remember the very spot in the road whilst in my carriage, when to my joy the solution came to me.' Yet the path by which Darwin reached this conclusion was a long and laborious one, and certainly his early years gave little hint of the development of genius. He was born at Shrewsbury in 1809, the son and the grandson of physicians. His grandfather, Erasmus Darwin, achieved considerable recognition for his poetical exposition of evolutionary views on the origin of species, similar to but achieved independently of those of Lamarck. Darwin's school-days made little impression upon him, although he became an avid collector of minerals and insects.

He himself has described these years in his autobiographical notes.

In the summer of 1818 I went to Dr. Butler's great school in Shrewsbury, and remained there for seven years. . . . Nothing could have been worse for the development of my mind than [this] school, as it was strictly classical, nothing else being taught, except a little ancient geography and history. The school as a means of education to me was simply a blank. . . . Towards the close of my school life, my brother worked hard at chemistry, and made a fair laboratory with proper apparatus in the tool-house in the garden, and I was allowed to aid him as a servant in most of his experiments. . . . The subject interested me greatly, and we often used to go on working till rather late at night. This was the best part of my education at school . . . but I was once publicly rebuked by the head-master . . . for thus wasting my time on such useless subjects. . . .

As I was doing no good at school, my father wisely took me away at a rather earlier age than usual, and sent me [October 1825] to Edinburgh University with my brother, where I stayed two years. . . . My brother was completing his medical studies . . . and I was sent there to commence mine. But soon after this period I became convinced . . . that my father would leave me property enough to subsist on with some comfort . . . [and] my belief was sufficient to check any strenuous effort to learn medicine. . . . During my second year at Edinburgh I attended Jameson's lectures on Geology and Zoology but they were incredibly dull. The sole effect they produced on me was the determination never as long as I lived to read a book on Geology, or in any way to study the science. . . .

After having spent two sessions in Edinburgh, my father perceived . . . that I did not like the thought of being a physician, so he proposed that I should become a clergyman . . . and [I] went to Cambridge after the Christmas vacation, early in 1828. . . . During the three years which I spent at Cambridge my time was wasted, as far as the academical studies were concerned, as completely as at Edinburgh and at school . . . [but] by answering well the examination questions in Paley, by doing Euclid well, and by not failing miserably in Classics, I gained a good place among the *οἱ πολλοί*, or crowd of men who do not go in for honours.

Yet in spite of his own somewhat melancholy assessment, Darwin's Cambridge years were to mark the turning point of his career, for there grew up a lasting friendship with J. S. Henslow, the Professor of Botany. It was Henslow who urged him to pursue the despised science of geology, which he did under Adam Sedgwick for an extra term at Cambridge after his graduation. It was also Henslow who arranged for Darwin to accompany H.M.S. *Beagle* (a 240-ton, ten-gun brig) on a survey voyage to South America and thence round the world. Henslow's parting gesture to the young Darwin was to suggest that he study carefully Lyell's newly published first volume of the *Principles of Geology*, 'but on no account accept the views therein advocated'. The five-year voyage was, for Darwin, a time of diligent observation and collecting, which gradually opened up a new

world of study before him, a world in which most of the treasures were geological and a world which (in spite of Henslow's warning) he saw through the eyes and studied by the methods of Lyell. 'I clambered over the mountains of Ascension with a bounding step', he wrote, 'and made the volcanic rocks resound under my geological hammer.'

Darwin returned to England in 1836, and at once set to work on the enormous collections of specimens which he had made. He had had little formal training in biology and Huxley considered his voluminous zoological notes to be almost useless. But his geological observations were very different, and even today they read as unusually comprehensive and perceptive accounts. Most of his zoological material was given to others to study, but he spent the next ten years working up his geological notes and specimens. In view of this early interest it is not surprising that much of Darwin's reasoning in *The Origin* was based upon geological evidence. It is therefore fitting to consider the Darwin–Wallace theory in the light of a century's geological knowledge, for in the fossil record alone there lies the opportunity to examine the course of evolution, and against this record evolutionary theories stand or fall.

But the occasion of this important centenary is not the only reason for my having chosen geology and evolution as the topic for this lecture. It is my privilege to be the fourth occupant of the Chair of Geology in this College, and I am very conscious of the debt which I owe to my three predecessors. The one dominating interest which they all shared, and to our knowledge of which each made a distinguished and lasting contribution, was the geological data of evolution.

The late Sir Arthur Trueman, F.R.S., stands undisputed as one of the most distinguished geologists of his distinguished generation. It was he who founded this geology department at the time of the opening of the College, and led it over the first thirteen years of its life. Within a short time Swansea became known, not only for the breadth and brilliance of Trueman's own research, but also for that of the group of students and research workers which he inspired to join him—such men and women as S. W. Rider, W. D. Ware, J. H. Davies, S. H. Jones, Emily Dix, R. O. Jones, and T. Neville George. Trueman's evolutionary contributions were many, but he will always be remembered for his demonstration and interpretation of the process of speciation in the fossil pelecypod *Gryphaea* from the Jurassic rocks of the Vale of Glamorgan. Few studies have had so profound an effect upon evolutionary thought.

Professor T. Neville George, one of Trueman's former pupils at this College, was appointed to the Chair of Geology in 1932. There could have been no more happy choice of a successor to Trueman, for Neville George not only shared his wide interests but also brought to his work the same great ability and indefatigable energy. Our modern knowledge of both the Carboniferous and the Quaternary geology of South Wales (on which the economy of the area chiefly depends) rests largely upon the work of Trueman and George. Perhaps the most important of Neville George's contributions to evolutionary studies are those in connexion with the process and pattern of changes at low taxonomic levels.

The late Professor Duncan Leitch had been one of Trueman's colleagues at Glasgow before he was appointed to the Chair in Swansea in 1947. His major contribution to evolutionary theory was the statistical demonstration of the nature and significance of infraspecific variation in fossils. To Duncan Leitch's wise and careful planning we owe most of the features of the superb accommodation which the department now enjoys.

His untimely death in 1956 was a grievous loss, not only to his family and to this College, but to the science of geology.

I make no apology for having spoken at length of these three men. Their contributions, both to the life of the College and to the topic of my lecture, are of the highest importance. It would, however, be improper to mention the development of geology at Swansea without reference to four others. Sir Franklin Sibly, the first Principal of the College, and a former Professor of Geology in what is now the University of Durham, contributed much to the department during its early years; Professor Alan Stuart, now of Exeter University, was a lecturer at Swansea for twenty-six years; Mr. Brian Simpson has been a lecturer in the department for the past twenty-eight years; and Mr. Trevor Marchant, the senior departmental technician, has been a member of the department since it first opened thirty-eight years ago. To the work and devotion of all these men we owe a debt that we can never adequately repay.

Darwin's Theory

Now although Darwin and Wallace first announced the theory of natural selection in 1858, it was the publication of Darwin's *Origin of Species* in 1859 that fully established it.

Other naturalists (Lamarck, Buffon, and Erasmus Darwin among them) had suggested descent with modification long before this, but the scientific world remained sceptical, and generally hostile. It was not until the eighteenth century that the true nature of fossils had been generally recognized, and its interpretation was governed by the widespread acceptance of Archbishop Ussher's chronology, which by detailed calculation from the Genesis narrative reckoned creation to have taken place in 4004 B.C. at 9.0 a.m. on 26 October. Because of this general climate of opinion the 'orthodox' view of creation had come to be based upon a theory of catastrophism, which maintained that the earth had experienced a number of successive cataclysmic revolutions (of which the Noachian deluge was the most recent). Each of these catastrophies was thought to have completely destroyed all living things, so that after an interval of time a new creation took place, whose beings were in turn entombed in the strata of the next cataclysm.

It is easy to smile at what we now regard as such a naïve concept—but it held undisputed sway in the scientific world for over a century, and found for its champions many of the greatest pioneers in the development of the natural sciences.

The importance of Darwin's work lies largely therefore not in the fact that he was the first to suggest the possibility of evolution, but in the fact that he convinced the great majority of scientists that evolution had taken place, and this he did by the presentation of a wealth of detailed data which supported his theory of the mechanism by which evolutionary changes had been effected. Darwin's theory of the origin of species by natural selection rests upon three essential observations. Firstly, he emphasized the infra-specific variation of organisms, both in their natural condition and under domestication, and appreciated that such variation may be inherited. Secondly, he demonstrated the prodigality of nature, by the high geometrical rate of increase of living things. 'Even slow breeding man', wrote Darwin, 'has doubled [his numbers] in twenty-five years, and at this rate, in less than a thousand years, there would literally not be standing-room for his progeny.' More recent estimates of this prodigality of nature amply confirm Darwin's views. The conger-eel produces 15 million eggs per season, the salmon 28 million eggs per season and the oyster may 'lay' over 600 million eggs, although fertilization is a matter of chance for the eggs are released into the water. It is estimated that if all the eggs of the oyster were to be fertilized and developed and this progeny multiplied, the great-great-grandchildren would number 66×10^{33}, and the shells of a generation would make a mountain eight times the size of the earth.

It was the interaction of the abundance of nature and infra-specific variation that provided the basis of Darwin's third observation—the action of natural selection. He argued that those organisms best adapted to their environment must, on the whole, survive and breed at the expense of the less well adapted. We now know that natural selection is to be thought of chiefly, not so much as a fierce 'nature red in tooth and claw' relationship, but rather as the production of differential reproduction which tends to involve systematic change in the gene pool of a population.

It is not my purpose to review the evidences of evolution. This was brilliantly done by Darwin himself, and his evidence has been supplemented by a host of examples provided by more recent students. It is rather my purpose to discuss some of the ways in which geology has added to our understanding of the evolutionary process.

Darwin himself recognized that his theory of the origin of species raised four major problems. These were the mechanism of the origin and inheritance of variations, the time factor, the origin of species, and the presence of gaps in the fossil record. The first of these problems has been largely solved by the studies of Mendel and succeeding generations of geneticists. The other three all fall within the province of geology.

Gaps in the Record— the Search for Missing Links

Darwin's first major concern with respect to the geological aspects of his theory was the nature of the fossil record. If evolution had really taken place then one should find evidence of it within every group of fossiliferous rocks, for these should provide petrified testimony to the truth of the process: a series of ciné stills on the broad film of evolutionary development. To Darwin's dismay they did not. Far from being full of evolutionary series, the rocks appeared to be full of gaps in the fossil record. Because of this many scientists remained sceptical, for here, if anywhere, was the final court of appeal. And so, one hundred years ago, there began the search for missing links.

Two distinct but comparable types of gap appeared to exist in the fossil sequence. Firstly, fossil organisms appeared in force in Cambrian strata, but the underlying Pre-Cambrian strata failed to yield more than a very few remains, all of which provoked dispute concerning either their Pre-Cambrian age or their organic nature or both. More than 500 species have now been described from the oldest fossiliferous rocks (the Lower Cambrian) and they represent a startling variety of forms (sponges, coelenterates, echinoderms, brachiopods, worms, molluscs, and arthropods). Thus all the major invertebrate phyla are known amongst the earliest fossils, and many of their representatives are relatively complex. If, however, one accepts on other evidence the theory of evolution, this 'sudden' appearance of such a varied fauna (displaying a Melchizedechian lack of ancestors, if not of descendants) is a glaring anomaly.

Darwin himself referred to the problem as follows:

> There is another and allied difficulty which is more serious. I allude to the manner in which species belonging to several of the main divisions of the animal kingdom suddenly appear in the oldest fossiliferous rocks. Most of the arguments which have convinced me that all existing species of the same group are descended from a single progenitor, apply with equal force to the earliest known species. . . . Consequently, if the theory be true, it is indisputable that before the lowest Cambrian stratum was deposited long periods elapsed, as long as, or probably far longer than, the whole interval from the Cambrian age to the present day; and that during these vast periods the world swarmed with living creatures. . . . To the question of why we do not find rich fossiliferous deposits belonging to these assumed earliest periods prior to the Cambrian system, I can give no satisfactory answer. . . . The case at present must remain inexplicable; and may be truly urged as a valid argument against the view here entertained.

Now what light has a century's intensive search of the older rocks thrown on this problem? The answer, surprisingly enough, is that the long and persistent search for Pre-Cambrian fossils, has proved almost, but not quite, fruitless.

Of those structures which are generally accepted as Pre-Cambrian fossils only two or three represent animals. The medusoid impression from the Algonkian of the Grand Canyon of the Colorado in Arizona probably represents a jelly-fish, and the Beltian Series of Montana has yielded a number of trails and burrows at least some of which are apparently of organic origin, as well as some possible (but disputed) remains of inarticulate brachiopods. Other Pre-Cambrian structures, once regarded as animal in origin and dignified by such names as *Eozoon*, *Protadelaidea*, and *Aitkokania*, are almost certainly of inorganic origin.

The evidence for the existence of Pre-Cambrian plants is also meagre, although it is a little more convincing. Walcott and others have described a variety of concentric calcareous algae from the Pre-Cambrian, but of these only one genus (*Collenia*) is now generally accepted as organic. Other concretionary structures of probable algal origin have recently been reported by McGregor from graphitic limestones of the 'Basement Schists' of the Bembesi gold belt in Rhodesia, and are probably more than 2,700 million years old. Rankama has shown that certain carbonaceous structures (*Corycium*) from the Pre-Cambrian of Finland have a C–12/C–13 ratio which is strongly suggestive of an organic origin. Various local Pre-Cambrian deposits of anthracite and graphite from Europe and North America, are regarded by many geologists as organic deposits and the extensive iron-ore deposits from both the Proterozoic and Archeozoic of the Lake Superior region, as well as others from Sweden and Brazil, may represent the action of iron-secreting bacteria. Tyler and Barghoorn have described primitive fungi and blue-green algae from the Huronian of southern Ontario, which are at least 1,300 million years old. Chert concretions from the Pre-Cambrian of Minnesota contain structures that have been identified as algae and fungi, and organic substances that yield what seem to be regenerated humic acids. This evidence, meagre as it is, at least proves the existence of Pre-Cambrian life and suggests that plants were antecedent to animals.

There remains, however, the formidable problem that the Pre-Cambrian fossil record is disappointingly poor in comparison with the richness of that of the Lower Cambrian. Three types of hypothesis have been offered to account for this disparity. Firstly, it has been suggested that Pre-Cambrian fossils did once exist, but have been subsequently destroyed by metamorphism and erosion. This must be rejected in the light of the number of areas where great thicknesses of unfossiliferous sedimentary rocks underlie the palaeontologically defined base of the Cambrian, without any unconformity or

apparent hiatus. A comparable type of suggestion that such fossils would probably be confined to abyssal deposits of which we have no record, is both biologically and geologically improbable.

The second type of hypothesis suggests that virtually no Pre-Cambrian organisms existed, the few we know as fossils representing exceptional cases. It is difficult to challenge such a conclusion based on negative evidence. That the host of Cambrian organisms developed without Pre-Cambrian ancestors appears on other reasoning to be most improbable, however. Two of the most convincing evidences of Pre-Cambrian life have arisen during the last decade from the application of new and sophisticated methods of geochemical investigation, and it would be rash to suppose that the extension of these studies will not contribute further evidences.

The third type of hypothesis supposes that the (presumed) Pre-Cambrian organisms were generally soft-bodied, and therefore incapable of preservation as fossils. Various chemical conditions (such as a high hydrogen ion concentration or an absence of calcium carbonate) have been attributed to the Pre-Cambrian oceans in order to account for an absence of hard skeletal parts. There are strong geological objections to most of these attributes, although it is still possible that the basic supposition is correct. Indeed the first appearance as fossils of such relatively simple groups as coelenterates and bryozoans appreciably later than that of relatively complex groups, such as arthropods, may lend some support to it. If this hypothesis should prove to be correct, it by no means removes the difficulty of the 'sudden' appearance of hard-shelled organisms in the Lower Cambrian, however, for this is almost as difficult to explain as the sudden appearance of organisms themselves. None of the explanations yet advanced to explain this is wholly convincing, yet there are a number of factors to be considered.

As G. G. Simpson has emphasized, it is somewhat misleading to speak of the 'sudden' appearance of most animal phyla in the Cambrian. The Cambrian system represents a very long period of time—about 80 or 90 million years—longer than any other system except the Ordovician: longer, in fact, than the whole Cenozoic era. Even the Lower Cambrian probably represents a period of 30 million years. The various phyla do not all appear in the oldest Cambrian strata, but rather 'straggle in' throughout its lower part. The evolutionary rates of change which such appearances demand are not excessive in comparison with those known from later chapters of the history of life.

That so many diverse animal groups should develop hard parts at even a roughly comparable period of time is remarkable, but not unthinkable. The present evidence of Pre-Cambrian fossils at least indicates that a number of lowly forms of life existed before Cambrian times —for how long these existed we do not know, but the earth probably became habitable for them at least as long ago as 2,000 million years. They may well therefore have reached a high degree of complexity and adaptability in such a time, and their diversity would be a selective factor (among others) in their apparently rapid development of hard parts. It may be, as Whittard has suggested, that some fundamental change in the cosmic rate at which chemical change produces energy was a major factor in allowing radial (as opposed to linear) evolution to proceed at such a rapid rate.

In summary then we may at least claim that the greatest gap of all in the history of life has been narrowed. A very few Pre-Cambrian fossils have been found, and, perhaps equally important, we now have a true sense of

the time factor involved. The earliest fossils known to us are still extraordinarily complex in comparison with the lowly organisms which must have represented the dawn of life. The ultimate gap will probably never be filled, yet even in those remote, and geologically dark ages, modern developments in geology, biochemistry, genetics, and physiology, throw a gleam of light on the possible origin of life itself. We may never know exactly how this came about but there seems no reason to postulate that organic change in Pre-Cambrian times was different in kind from the type of change observable elsewhere in the fossil record.

The second type of gap in the fossil record was that to which Darwin referred as 'the absence of intermediate varieties'. 'Why', Darwin wrote, 'is not every geological formation and every stratum full of such intermediate links? Geology assuredly does not reveal any such finely graded organic chain; and this, perhaps, is the most obvious and serious objection which can be urged against the theory.' Darwin believed the absence of such forms to be the result of the imperfection of the geological record, the lack of study of strata of many ages in most parts of the world, the slow rate of speciation, and the conditions under which it occurs, and the fact that two forms between which one might expect to find an intermediate link, may both have developed from a common, but distinct, ancestral form.

Modern geology has amply confirmed Darwin's views. The once allegedly 'natural' breaks between systems and formations are continuously being found to be bridged by transitional deposits in other areas, and the effects of local disconformity, hiatus, selective preservation, facies variation, and migration have been shown to be every bit as important as Darwin had supposed. New faunal, physical, and geochemical methods of analysis show even the most apparently uniform series of strata to be commonly interrupted by non-sequences.

But modern geology has not only confirmed Darwin's views concerning the absence of many intermediate forms: it has also made enormous strides in filling many of the major gaps in the record, and has provided sufficient examples of both infra-specific and infra-generic evolutionary sequences, as well as those at intermediate levels, to indicate the general pattern which such changes follow. Within fifteen years of the publication of *The Origin* the graded sequence of equid evolution had been brilliantly unravelled by Kovalevsky in essential correctness and later interpreted by Marsh and Huxley. Rowe's classic study of the evolution of the echinoid *Micraster* in the English Chalk was published in 1890 and has been followed by a number of other studies, all of which provide conclusive evidence of gradual morphologic changes in chronological sequences of populations. So continuous have such changes proved in diverse groups of diverse age that it is difficult to see how the evidence for evolution could be made more convincing. It would be difficult, for example, to demonstrate conclusively, that the camels living today are the direct descendants of those which lived two or three hundred years ago, yet no reasonable person would dispute the suggestion. It may be fairly said that much of the geological evidence for evolution is of this type.

At intermediate taxonomic levels many of the newly discovered ancestral forms are almost identical with the postulated forms which palaeontologists had predicted. A very striking case is that of the ancestors of the Permian labyrinthodont amphibians. Watson, in the 1937 Silliman lectures at Yale, discussed in detail the characters which one would expect to find in the then unknown animal which was the ancestor of *Eryops*, basing his

predictions on the extrapolation of evolutionary trends in the labyrinthodonts as a whole. Five years later Romer and Whitter described a fossil amphibian from Texas, which occurred in strata underlying those in which *Erypos* was common. The newly discovered amphibian, though not itself the ancester of *Eryops*, is clearly of a closely similar type and in every point it agrees with Watson's predictions.

It would, however, be wrong to convey the impression that all or even most of the gaps in the fossil record have been filled. It remains true that representatives of most new minor taxonomic categories, and almost all the major taxonomic groups, appear suddenly in the fossil record, without ancestral transitional forms. Our knowledge of existing transitional sequences, and our understanding of the processes and hazards of fossilization, are now such, however, as to suggest that it is far more probable that the unfilled gaps represent similar unknown transitional sequences, rather than sudden saltations. Most, but not all, palaeontologists accept this conclusion, and regard the absence of many intermediate forms as a result of such factors as sedimentary non-sequences (as in Brinkman's ammonite sequences, where it has been shown that an apparent evolutionary 'break' is the result of the non-deposition of only one inch thickness of shale), faunal migration (as in the horses), and the probability that the most profound and rapid morphological changes occurred in small isolated populations.

In summary then, some gaps are filled: many remain; but the weight of palaeontological evidence confirms Darwin's view that they are gaps which mark not the total absence of intermediate forms, but rather their lack of preservation. The fossil record is so imperfect a representation of the hundreds of millions of extinct species, and even as such is so imperfectly known, that the wonder is not that many gaps in it exist, but rather that so relatively many transitional sequences have been described.

THE ORIGIN OF SPECIES

Although Darwin's book was entitled *The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*, he was, in fact, unable to do more than suggest ways in which the interaction of variation and abundance in organisms and natural selection might produce divergence. His suggestions were supported by a host of carefully reasoned observations on such things as variation under domestication, but a major weakness remained in his argument until it became possible to show that what was plausible, or even probable, had, in fact, taken place. In Darwin's time no one had yet demonstrated the origin of species. The chief limitation in all studies of living organisms is still the impossibility of tracing them over periods of time of sufficient length for significant evolutionary changes to take place. It is only during the last few hundred years that organisms have been subjected to systematic study, and only in a few cases that any changes in them have been observed. All such changes are of a very minor kind, however, and in spite of the combined efforts of domestic breeding and other more strenuous artificial methods of selection, no new species have yet been produced. Nor is this surprising, for we now know that in nature the transition from one species to another often takes 500,000 years or more (ignoring the problems of asexual organisms and polyploid plants, which are not typical of organisms in general). Such a period of time lies wholly outside the limits of experimental studies, and even if it should prove possible to reduce it drastically

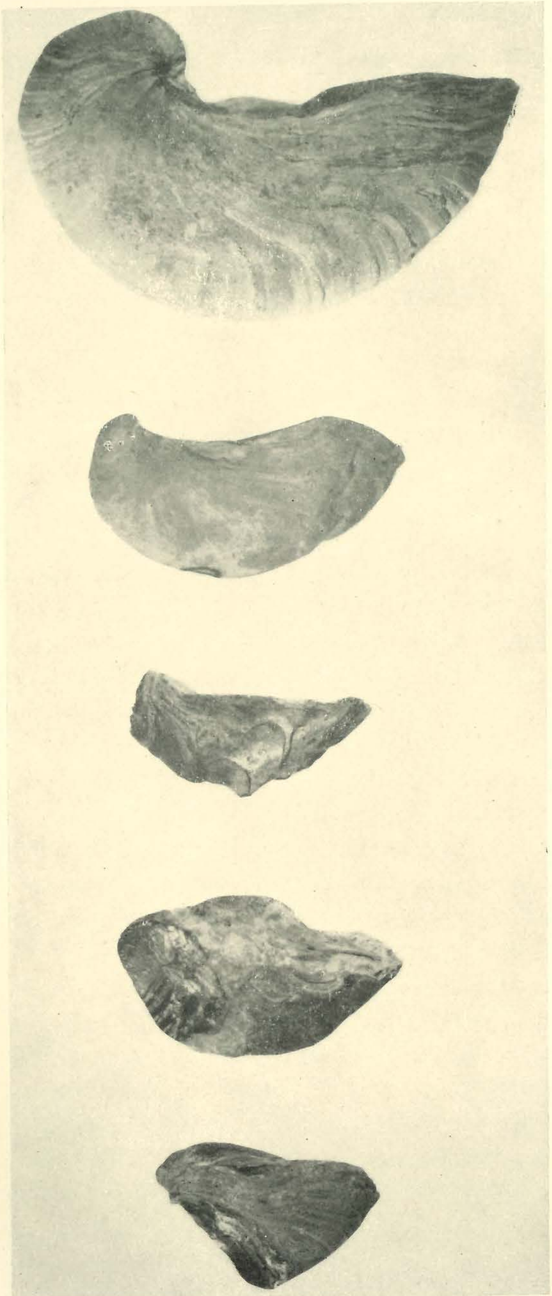

FIG. 1. The evolution of *Gryphaea*. A collection of specimens made by the late Sir Arthur Trueman, F.R.S. to illustrate his study of *Gryphaea*. The geologically older specimens on the left, younger on the right.

by artificial methods, we should still remain unsure as to whether these induced changes bore any resemblance to those which have taken place in the natural development of life on the earth.

In the fossil record alone there is the opportunity to study the whole process of speciation, as opposed to the small fragments of it which are susceptible to neontological studies. Admittedly it lacks many important details—it provides only indirect and more or less limited information concerning such things as the soft parts of organisms, their genetics and ecology for example, but it has the unique advantage of providing occasional records (albeit fragmentary) of ancestor–descendant series of populations over sufficiently long periods of time for new species to develop.

The process of speciation has now been demonstrated in fossil representatives of most of the major taxonomic groups of widely different ages. One example must suffice. I select it, not only because it is one of the most fully documented and critically studied of all, but because of its intimate association with Sir Arthur Trueman and with this College and county. The example is provided by the evolution of the pelecypod *Gryphaea*, which was first suggested within six years of the publication of the *Origin of Species*. The example remained neglected and largely unknown, however, until Trueman's brilliant studies in the 1920's. These studies have recently been subjected to some criticism, but they have not yet been shown to be in need of any major modification. *Gryphaea* was a coiled Mesozoic oyster which flourished over a wide area and which arose from the genus *Ostrea*. It has been shown in fact, that this gryphaeoid development from the stable *Ostrea* stock occurred independently on a number of different occasions in the Mesozoic. Trueman made a detailed study of the development of *Gryphaea* through

300 ft. of Jurassic strata in the Vale of Glamorgan, and tabulated the detailed changes in a number of characters. One of these, the coiling of the left valve of the shell, is shown in Fig. 2. The curves, which represent frequency curves for successive populations, are all essentially unimodal, and indicate that we are dealing with a series of single homogeneous populations. Now the 'typical' *Gryphaea* is quite unlike the 'typical oyster' ancestors from which it descended. It is larger, thicker, strongly coiled, and has a very reduced area of attachment on the shell. These differences are clearly shown in Fig. 1. Yet between the two genera, there exists a complete transition. There can be no more convincing proof of the evolutionary process than this series of successive populations, each one slightly different from its predecessor in the mean characters of its members. They form an overlapping and beautifully graded series in which, although successive communities are closely similar, the curves of the first and the last members of the sequence show no overlap, or, in other words, they are morphologically and taxonomically distinct. In such a series the neontological concept of a species loses all objectivity, for it is but an arbitrary stage in an essentially continuous graded series.

Although the *Gryphaea* sequence of changes is probably more rapid and morphologically profound than most others, enough is now known of other examples of comparable sequences to indicate that it is typical of the pattern of evolutionary change, although there are countless variations upon it. This then indicates the origin of divergence. But living species are marked not only by divergence, but also by discontinuity. The development of this discontinuity, though not illustrated by *Gryphaea*, is well illustrated by other organisms, both living and fossil, such as Brinkmann's ammonites for example. The general discontinuity between living species arises

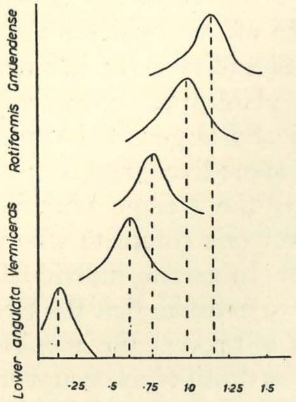

FIG. 2. Frequency curves of variation in coiling (expressed in number of whorls) in left valves of *Gryphaea* populations from successive levels in the Lower Lias of the Jurassic of Glamorgan. Liassic subzones are plotted on the *y* axis. (After Trueman)

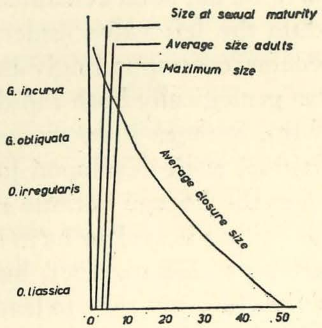

FIG. 3. Time changes in average size at shell 'closure', maximum size, average adult size, and size at sexual maturity in the *Gryphaea* evolutionary sequence. Size in centimetres is plotted against characters of successive species; species are plotted in ascending order of appearance. (After Westoll)

primarily as a result of geographical isolation of infraspecific populations which may ultimately produce hereditary differences between them. The degree of discontinuity depends largely on the length of time of separation, and if this is sufficiently long, the two groups will become reproductively isolated and give rise to new species.

But the *Gryphaea* sequence not only demonstrates the evolutionary pattern; it also provides an insight into the the evolutionary process itself. The question of questions in such evolutionary series as this is, 'How are such evolutionary changes triggered, directed, and maintained?' Now one of the most striking things about the development of the several *Gryphaea* series in the Mesozoic is that each of them exhibited the same general trends;

trends which are also reflected in the ontogeny of geologically younger individuals. In all of them the right valve of the shell remained small and more or less flat, while the left valve underwent planispiral coiling, and became correspondingly thicker and larger. This trend was geologically both rapid and short-lived, and in each of the lineages it continued until the average adult individual shell developed just over one complete whorl, when the lineage became extinct. In certain individuals the coiling is said to have been so extreme that the two valves pressed together, tending to prevent the opening of the shell and thus to lead to the death of its occupant.

Palaeontologists were not slow to generalize from this particular case, for here, if anywhere, lay a major clue to the mechanism of evolution. 'Here', it is argued by some, 'is a supreme example of the inner evolutionary urge, the relentless power of developmental momentum, the inevitability of orthogenesis.' According to this claim, the coiling of the shell was either non-adaptive, or if originally adaptive was continued to such extremes that it resulted in racial extinction. It was the acceptance of this interpretation that led to the concepts of 'neovitalism' and 'programme evolution'. For clearly if this interpretation is valid, then Darwin was greviously wrong in his estimate of the role of natural selection in evolutionary change.

There is growing evidence, however, that both the underlying assumptions in this interpretation are false. Far from being non-adaptive, the development of coiling appears to be a highly adaptive modification to life on the muddy sea floors on which *Gryphaea* flourished. It first raised the shell aperture from the mud and later allowed a sessile but free mode of life. Although it is not clear that this was a response to increasing muddiness in the ancient Jurassic seas, it is entirely possible that it

was a more perfect adaptation to an essentially stable environment. In either case it is difficult to regard the coiling of *Gryphaea* as anything other than adaptive.

Nor can we regard this evolutionary series as an example of an adaptive trend gaining 'such momentum that it dooms the race to extinction'. There was linked with it the common adaptive trend towards increase in size, and recent studies by Westoll have related this to the coiling (Fig. 3). Westoll expresses the degree of curvature of the shell by a plot of the average size at which continued coiling would close the shell. In the earlier, feebly coiled forms, this size at closure was never approached, but in later forms the rapid increase in coiling entailed a correspondingly rapid decrease in the closure size. The combined effect of this with the size increase, was such that some later individuals, so it is claimed, were closed up and killed off. Now I have personally never seen such a specimen, but it appears that they were virtually all larger (and therefore essentially older) individuals, and this was by no means necessarily an unfavourable factor in the life of the community. It may in fact have been a decided advantage, for it could have served to remove the 'unproductive' members who had passed their reproductive span. 'It is', as Simpson has rightly remarked, 'one of the radical differences caused by the development of social structures that in these the non-breeders and those past breeding age may have a decided influence on the evolution of the group.'

The true limit of these two adaptive trends is clearly defined by the point at which shell closure commonly takes place before full sexual maturity. Although this limit was very closely approached in *Gryphaea incurva*, it does not appear to have been passed, but it was clearly one of perhaps several factors which gave the group a precarious existence. It would be unjustifiable, however, to infer that this trend alone extinguished the race.

So the fossil record provides glimpses of the origin of species—a broad review of the pattern of evolution, and the pattern proves to be one of slight but cumulative and continuous change. But more than this, the fossil record allows us partially to interpret the process of evolution; a process which, so far as we can read the record, involves the delicate interaction between natural selection and inherited variability. And this is the process which Darwin and Wallace first predicted a century ago.

Now although species arise in this way, we may well ask whether such minor changes are adequate to bring about the major structural changes that have marked the developing pageant of life. Can it really be so simple as this? Can an odd mutation, a minute variation, a slight advantage, be adequate alone to effect the changes the earth has seen? Can one seriously believe that so feeble a mechanism can produce such mighty results? The lowly life of the seas that bore the first living creatures—the hosts of shellbound invertebrates that thronged the shores of those ancient lands—the darting shoals of armoured fish that marked the advent of a new level of complexity in body structure—the clumsy squat amphibia that recorded the first tenuous conquest of the land by vertebrates—the swamps of lofty trees that once gave shade to this very countryside—the dinosaurs, hideously strong, as they thundered across the pages of time—or in more familiar things—the flower of a lily, the fragrance of a rose, the flight of a swallow, the face of a child—can it really be that variation and selection, these mechanisms alone, can produce such wonders as these?

We are tempted to deny it—but one final factor has yet to be assessed—and that is the factor of time. With the help of time, adequate time, an eternity of time, what then?

TIME

An interest in time and the age of the earth is almost as old as man himself, as many ancient civilizations bear witness. The Brahmins of ancient India believed the earth to be eternal, Babylonian astrologers deduced that man had appeared half a million years ago, and the Persian Zoroaster taught that the earth was 12,000 years old. As long ago as 450 B.C. Herodotus had suggested that the rate of deposition of sediment by the Nile, indicated that the building of its delta must have required many thousands of years. In Darwin's day, however, there was no reliable method of measuring geological time, although the relative ages of most strata were generally known, and it is only during the past three decades that new methods have provided a dependable scale of geological time. The results obtained have been of the greatest importance to the study of evolution. 'It may be objected', wrote Darwin, 'that time cannot have sufficed for so great an amount of change, all changes having been effected slowly' and although he argued that the Principle of Uniformitarianism demanded a far greater span of geological time than most admitted, he could produce no quantitative estimate of such a period.

In the 1890's Lord Kelvin suggested that the earth was probably not more than 20 to 40 million years old. This estimate was based upon a study of the rate of cooling of the earth, by which it could be shown that, even if the earth was originally enormously hot, it would cool to its present temperature within such a period of time. Similar studies of the sun confirmed this figure. Clearly, if all the sun's energy resulted from its cooling and shrinking, this estimate was reliable. This was a setback to evolutionists, who found it difficult to accept the compression of the earth's physical and organic history into so brief a span. Studies of the sodium content of the oceans, however, suggested an age of about 100 million years. This calculation was based upon the assumption that all the sodium chloride in sea water has been derived from the weathering of igneous rocks, that is, that the seas were originally 'fresh water'. The figure was derived by dividing the estimated total mass of sodium in the oceans by the average annual increment from rivers and streams. We now know that this is a very inaccurate determination and all the corrections that need to be applied tend greatly to increase the estimate of the time involved. Similar problems and inaccuracies arise in the attempt to calculate the age of the earth on the basis of the total thickness of sedimentary rocks.

Here then were two types of estimate which provided significantly different ages for the earth: the one, apparently incontrovertible, giving a figure of the order 20–40 million years: the other, suggesting more than twice that maximum figure, yet being subject to major corrections all of which tended substantially to increase it.

The impasse was not finally resolved until the discovery of the radioactive disintegration of uranium by Becquerel in 1896, which proved the existence of a completely unsuspected source of energy for which Kelvin's estimate had made no allowance. But curiously enough, Becquerel's discovery had another, much more important effect upon the measurement of geological time, for it initiated a new field of study which revolutionized concepts in physics and chemistry and ultimately provided a new type of geological clock. The process of radioactive disintegration affects certain elements having unstable atomic nuclei, which undergo spontaneous constant disintegration to form more stable end products. Thus uranium, for example, breaks down to give lead

and helium. The rate of this disintegration has been measured with a high degree of accuracy and has proved to be very slow and, like all such disintegration, totally independent of all known environmental conditions, none of the physical and chemical variables which affect most reactions having any apparent effect upon it. Now certain uranium and other radioactive minerals are fairly widely distributed in igneous rocks although they are almost always found in small amounts. If therefore the ratio of 'disintegrated' lead to 'undisintegrated' uranium is measured, it is possible to calculate the age of the rock. Although there are a number of complications involved in such determinations, they have now provided a reasonably dependable scale of geological time, and they have recently been supplemented by studies of radiogenic lead-thorium, rubidium-strontium, potassium-argon, and carbon isotope ratios.

These successive studies have steadily pushed back the age of the oldest known rocks. The most recent refined strontium experiments show a maximum age of about 3,300±300 million years for various lepidolite-bearing pegmatites in Rhodesia, Wyoming, and Manitoba, although other methods of analysis of the same rocks suggest a rather smaller age (2,700 million years). Preliminary studies suggest still greater ages for other rocks from Swaziland and the Transvaal. Indeed, the Rhodesia–Manitoba pegmatites are themselves part of a granitic suite of rocks that is intruded into a considerable thickness of still older rocks. The most recent estimate of the age of consolidation of the earth's crust is 4,200 million years (±10 per cent.). This, of course, is not the age of the earth, which is somewhat greater.

The combined studies of physicists, chemists, geologists, and astronomers on meteorites, rocks, and the rate of expansion and present distance of the earth from various outlying galaxies (especially M–31) all tend to suggest an age of 4,500–5,000 million years for the earth itself. The mind of man reels at such an 'eternity' and it reels no less when it seeks to grapple with both the physical and the philosophical problems of those dark ages. There are some who suggest that such a distant date represents not only the time of origin of the earth, but also of an unimaginably greater 'cataclysm' in which the cosmos, and perhaps even matter itself, came into existence. Others, however, interpret the apparent expansion of the universe quite differently, and suggest that it implies a continuous creation of matter. 'May it not be that it is a property of space', Littleton asks, 'that wherever space occurs then matter may appear in it *from nowhere*, and to just such an extent in total throughout the observable universe as to balance the loss over the frontier horizon of the universe?' Clearly, therefore, whichever of these two hypotheses proves to be correct, the question of the age of the earth inevitably leads us to the fundamental question of the origin of matter itself—and even this, once the most profound and inscrutable of all questions, now approaches the threshold of scientific study. So ancient is the earth on which we dwell—ancient almost beyond our imagining: so profound and as yet so obscure are the problems of its origin—and yet they impinge upon every phase of man's experience and knowledge.

We know nothing of life in other parts of the vastness of the universe. It is not impossible that within its uncharted emptiness, other bodies than ours may support living things. It is not impossible that 'life' on other bodies may be utterly unlike anything we can conceive, so unlike it, in fact, that even our use of the word 'life' itself may be quite inappropriate and our description might demand a new vocabulary. But on our own planet

there is life and we know something of its history. The earth is about 4,500 million years old, but for the greater part of this enormous period of time there are virtually no fossil remains; in fact, undisputed fossils appear in quantity only in Lower Cambrian times, about 500 million years ago, that is, during what may be only the last ninth or tenth of the earth's life. Even this fragment of geological time is almost unimaginably long, however. Suppose that an imaginary tree growing at the rate of $\frac{1}{10}$ inch every thousand years, had been planted at the dawn of Cambrian time and had continued to grow ever since. It would now be almost a mile high, more than four times the height of the Empire State Building. A similar tree planted when our own species appeared would be a mere 2 feet in height, and one planted at the time of Christ only $\frac{1}{5}$ inch.

Now this scale of time is of enormous importance to the theory of evolution for it allows ample time for the postulated slow evolutionary processes to have taken place. No longer may 'it be objected that time cannot have sufficed for so great an amount of change'. But it can also provide information of a quite different type, for it affords a scale against which it is possible to make approximate measurements of rates of evolutionary change.

Evolutionary rates may be expressed in terms of genetic, morphologic or taxonomic change, and, in the two latter cases, palaeontology provides the only available data. Detailed studies in this field, in spite of many limitations, such as, for example, the 'monographic bursts' of Cooper and Williams, are of the greatest interest.

Thus the inarticulate brachiopod *Lingula* has apparently undergone no substantial change since it first appeared in the Ordovician 400 million years ago, whereas the enormous diversification of the mammals has taken place within less than 80 million years. Simpson has provided striking illustrations of similar, but less obvious, differences in his analysis of survivorship curves of genera of various fossil groups.

But such studies can also provide a clue as to the explanation of some of these differences in evolutionary rates, since they appear to depend largely upon the intricate interaction between the organism and its environment. An excellent case in point is the marked changes in equid morphology during Miocene times, which has been shown to correspond with changes from browsing to grazing habits. It is not without significance that the first appearance of fossil grass seeds is in the Miocene flora of the High Plains. The effect of this mid-Tertiary development of the grasses, and the general transition from hardwood forest to open prairie, was of overwhelming importance in the evolution of the mammals and an understanding of it is fundamental in the interpretation of their evolutionary trends.

There are, however, other problems and implications which arise when one considers evolution against the background of geologic time. The average time involved in specification during the adaptive radiation of the mammals was probably of the order of 500,000 years, while the average rate of change in most morphological characters, even in 'rapidly evolving' groups, is very slow. Simpson has shown, for example, that the average change in diameter of early equid molars, is less than 0·2 mm. per million years, while differences of 3·0 mm. or more were present within single populations. These rates of change are thus so slow in most groups that it is generally quite impossible to observe such 'natural' (as opposed to artificial) change in contemporaneous faunas. This readily answers those who complain that no one has ever seen a new species develop. Yet, slow as these rates of

change are, the length of time over which they have occurred is so great that even such imperceptible changes mark the origin of new forms of life.

Here then is the final factor. Here we may conclude our review of the testimony of geology to the theory of Darwin. Its evidence has carried us far, as far as the depths of space, as far as the origin of matter, as far as the dawn of life, as far as the limit of time.

Here is the origin of species, here is the pattern and the process of evolutionary change, here is time beyond the vistas of our level of perception, here is the great unfolding pageant of life on the earth, and here is Darwin, fully and triumphantly vindicated.

The Meaning of Evolution

But if the last hundred years has brought a fuller understanding of the mechanism of the evolutionary process, it is no less true that it has also brought a fuller understanding of its meaning. Perhaps the most remarkable thing about the publication of *The Origin* was not the reception which it received from the scientific public, but the worldwide convulsion and outburst which it produced amongst men of all interests and persuasions. Philosophers, politicians, theologians, literary critics, historians, classical scholars, and the man in the street—all alike took it upon themselves to assess its worth. And as so varied a group studied it, so their verdicts also varied—some accepted and respected Darwin's conclusions, others viewed them with suspicion, but most rejected them out of hand, and denounced both Darwinism and all its supposed implications. 'As for the book, some treasured it, some burnt it, and some, undecided, like the Master of Trinity College, Cambridge, merely hid it!' Scientific theories, philosophies, political systems, ethical standards, revolutionary movements, social reforms, and economic *laissez-faire*—all these and more were established, modified, or justified upon Darwin's premises. Indeed Darwinism soon became all things to all men.

In our own day, a century later, Darwin's theory, having found its place and left its mark in a host of different fields of inquiry, is now seen in its true perspective, and most of the clamour has subsided around it. The uninformed condemnation and hostility on the one hand, and the extravagances of many popular science writers on the other, have both been largely forgotten. There is perhaps only one area of human activity in which misunderstanding persists, for in the realm of religious belief evolutionary theory still poses an 'unresolved conflict', as Dr. David Lack called his most recent book.

It was organized Christian religion which came into the most conspicuous collision with the early views of evolution. But why was this so? Certainly the notion of evolution was not new. Lyell had demonstrated it in the development of the earth, Kant and LaPlace had suggested it in the origin of the solar system, Lamarck in the development of life, Herder in history. Some of these theories clearly contradicted the generally accepted interpretations of the Genesis narratives of creation and yet none of them occasioned a fraction of the fury that marked the publication of Darwin's book. For it was not fundamentally an attempt to vindicate a particular interpretation of the early chapters of Genesis that led to the bitter controversies between leading scientists and churchmen. What many devout Christians feared was the apparent common tendency of these new hypotheses to remove the hand of God from the course of events in the material world. Amidst such fears the *Origin of Species* appeared to many as the ultimate challenge.

And yet the truth is that the theory of evolution is neither anti-theistic nor theistic. So far as religion is concerned it is strictly neutral, for it is a theory of the mechanism of descent with modification which seeks to explain *how* new species arise. It does indeed correct certain former ideas of the manner of creation, it does suggest that natural selection proceeds by natural laws, but like all other scientific theories, it provides no interpretation of natural laws themselves, for it no more proves them to be the result of pure chance, than it proves them to be the servant and expression of purpose.

This conclusion should not surprise us, for it is true of science as a whole. And the neutrality arises, not because of some inadequacy in evolutionary theory, but because the student of evolution deliberately excludes from this explanation all reference to final causes. Unlike his Greek predecessor he concerns himself not with the question 'Why did life develop?' but with the question 'How did life develop?' To this latter question we now begin to understand the answer. But the mind of man is such that, even as we understand the 'How?' of life, we gaze towards the ultimate 'Why?' To that question evolutionary theory gives no answer.

This need not and does not imply that the question 'Why?' is meaningless or irrelevant. It means only that we must look elsewhere for the answer, for the questions 'How?' and 'Why?' are not alternative and competitive, but rather complementary to one another. And this complementary relationship, which it has taken a century for the world to assimilate, brings us back to Darwin, for it is brilliantly summarized by the three short quotations from Whewell, Butler, and Bacon with which he prefaced the *Origin of Species*.

Darwin concluded the book with these majestic words:

Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

And so the evolutionary process continues, for it is never static. Even now new species, new ways of life are gradually unfolding, and yet there is one great difference. For the first time in the history of life on the earth, a species has arisen with the power largely to control the future pattern of evolution. It is a power that confronts mankind with a challenge that provides at once both an inspiration in the endless change and progress that could be produced, and a sense of horror in the prospects of failure that may follow our infraspecific strife. And if the question 'How?' is neutral in the search for the 'Why?' of ultimate meaning, this question 'Why?' is critical in the response of mankind to the challenge of the future.