

Introduction: Forty Years Later

THE BOOK NOW BEFORE YOU was written intermittently from 1938 to early 1942, when its writing was interrupted by overseas service in the army. As noted in the preface, its final preparation, not requiring rewriting, was completed in my absence by my wife, some staff members at the American Museum of Natural History, and the staff of the Columbia University Press. The present edition is thus being published more than forty years after the book was written. Except for the addition of this new foreword, the book is here reprinted without any change from the first printing. The purpose of this new foreword is to outline briefly some antecedents of the book, its place in the study of evolution as a whole, its effects on such studies as far as the author can judge, and something about developments not foreseen or foreseeable forty years ago.

In 1894 a Columbia University Biological Series of books was started under the editorship of Henry Fairfield Osborn, then a professor at the university. Early volumes under that sponsorship and editorship were published by the Macmillan Company, as Columbia did not then have publishing facilities of its own, only an editorial board. The first volume in the series was *From the Greeks to Darwin*, written by the editor, Osborn, on the basis of lectures given at Princeton and at Columbia. Although Osborn was a paleontologist, this volume is concerned with the history, not particularly paleontological, of the concept of evolution.

As its title indicates, the first book in the Columbia Biological Series was devoted to the thesis that evolutionary concepts, both philosophical and biological, themselves have evolved from the ancient Greeks, many of whom Osborn specified from Thales (born in 624 B.C. according to Osborn, more probably about 636 B.C.) to Galen (born A.D. 131 according to Osborn, somewhat dubious but probably close). Traced on through the centuries, the concept is seen as reaching its full development by Darwin and by Wallace, whom Osborn considered essentially post-Darwinian. (Wallace was still living and writing when Osborn wrote this book.) Osborn ended his book with the statement that only the future can determine whether (as of 1894) the "old, old problem" (of the causes of evolution) had been

fully answered or "whether we should look for still another Newton in our philosophy of Nature." Historians of biology, more pertinent here than the majority of historians of science, who usually have stressed the physical sciences or confined themselves to them, have modified or rejected Osborn's thesis of a continuous evolution of evolutionary thought from Thales to Darwin, or Wallace, or to Osborn himself. I agree with what I think is the present consensus of historically minded biologists or biologically minded historians. Lamarck's theory was not supported by objective evidence, and like all scientists he inherited a body of facts, conjectures, and theories, but Lamarck was the first to be explicitly and completely committed to an evolutionary concept of the history of life.

Not only after Lamarck but even after Darwin (whom Osborn had met when Darwin was old and Osborn young), Osborn said, as previously noted, that another Newton was needed to solve the problem of an evolutionary philosophy of nature. In later years it seemed probable that Osborn had come to think of himself as the other Newton. As a continuation of what he thought of as a tradition continuous from the early Greeks, he sought a more explanatory theory of evolution. He developed this in a series of papers, especially in the 1910s and 1920s, and in the two massive memoirs, on titanotheres (1926) and proboscideans (published posthumously in 1936 and 1942), to which he devoted much of the last decades of his life, beginning as early as 1910. (He died at the age of 78 years on November 6, 1935.) His final views were especially set out in a series of papers devoted (under this title and some others) to "The Origin of Species as Revealed by Vertebrate Paleontology." The gist of his theory was first called "rectigradation" and later "aristogenesis." This was defined as "the gradual, secular, continuous, direct, reactive, adaptive origins of new biomechanisms" in what he first called the "germ-plasm" and later the "geneplasm," which did not refer to genes in the now usual genetical sense. (The word "gene" had already been used by T. H. Morgan in its present sense in 1917.) As to the modes of the origin of biomechanisms, Osborn concluded that "We are now on absolutely sure ground. This ground is contra-Lamarckian and contra-Darwinian. It is also contrary to the neo-Darwinian evolutionary hypotheses of the leading biologists and geneticists of our day."

The "absolutely sure ground" was paleontological observations and

deductions, especially those Osborn made from his studies of titanotheres and proboscideans, among other fossil mammals. In his final years, Osborn was aware that his theory was not accepted by most paleontologists or by other biologists. He consoled himself with the belief that it would be accepted sooner or later. It has not been.

Osborn obviously was not the first paleontologist to relate the fossil record to evolutionary theory. Darwin was a geologist and paleontologist before he overtly espoused evolution, and two chapters in *The Origin of Species* are devoted primarily to paleontology. Apart from that, Edward Drinker Cope (1840–1897), personally known to Osborn early in Osborn's career and in the last years of Cope's, had been a convinced evolutionist. He published two books mainly devoted to paleontology and evolution: *The Origin of the Fittest* (1886) and *Primary Factors of Evolution* (1896). In his long biography *Cope: Master Naturalist* (1931) Osborn stigmatized Cope for being a Neo-Lamarckian and for inventing new terms such as "catagenesis." There is irony in this, for despite his claim to be "contra-Lamarckism" there was a strong Lamarckian element in Osborn's theory, and he was also prone to invent new terms, like "aristogenesis."

All this is relevant, at least indirectly, to the book here reprinted with this new foreword. There is also a curious connection. At the opening of a new building for the Peabody Museum at Yale University in December 1925 Osborn gave an address in which he said; "Perhaps within the very walls of the Peabody Museum, where adaptation is set forth so transparently by the master hand of Lull, some young Aristotle or Darwin may find his inspiration to grasp the problem of the origin of species which has baffled man for two thousand five hundred and eighty-five years." (He must have been counting from 660 B.C., which would have started the search even before Thales.)

It is quite obvious that I am not a Darwin, and still less an Aristotle, but it happened that a bit later in the year (1926) when that statement of Osborn's was published I became a Ph.D. after studying in the Yale Peabody Museum under the tutelage of Richard Swann Lull (1867–1957). Lull was another of the then increasingly numerous paleontologists interested in evolutionary theory. He was Neo-Darwinian in general, especially as regards the reality and importance of natural selection, but he tended to give almost equal time

to opposing or marginal opinions that he considered unlikely but not impossible. Not much later, from 1927 to 1935, I was closely associated with Osborn at the American Museum of Natural History.

Before joining the American Museum's curatorial staff, I had published twenty-five papers and finished writing two large memoirs on Mesozoic mammals later published as hardback books by the British Museum (Natural History) (1928) and Yale University Press (1929). Obviously these are now outdated, but they are still found useful and have recently (1980) been reprinted together in a single volume. On the American Museum staff I had on hand an even greater collection of fossils than at the Yale Peabody Museum, and I was launched into more varied descriptive and taxonomic studies mainly of fossil mammals. I was also almost immediately involved in field work, finding and collecting fossil vertebrates, especially mammals. Even on the basis of what I then knew, I was firmly convinced that evolution is a fact, obvious to anyone really acquainted with the evidence. Of course I have remained so ever since, all supposed evidence to the contrary being absurd or, less commonly but sometimes, simple prevarication.

As a result of training and experience, I also habitually thought in four dimensions, time being the fourth and being particularly paleontological. I was sometimes astonished to find that nonpaleontological biologists did not all think in this dimension as well as the physical three. I had read *The Origin of Species* and some others of Darwin's books and many papers on evolution, as well as straight paleontology, in English, French, and German, the latter two, in that order, having been required for my Yale degrees. I also had the advantage of having spent most of a field season (summer 1924) alone with William Diller Matthew (1871–1930). He was a great paleomammalogist, a hero to me, and with him familiarity bred only respect and admiration.

Of course I also read most of the work of Osborn, whom I thought and still think of as "The Professor." I respected and admired him too, but admittedly in a somewhat lesser way. As his theoretical views were developed while I knew him, they seemed to me to become more vague and his "absolutely sure ground" in paleomammalogy to become rather a quagmire. He knew that I disagreed, but he did not resent disagreement if it was courteous, and he probably expected

that I would come around to his views as I learned more. I was intensely interested in evolutionary theory, but for about my first ten years there I did not think I knew enough to judge extant theories well or perhaps even to add something to them. I was inclined toward Neo-Darwinism to the extent of considering natural selection as the principal but not necessarily the only nonrandom or directive element in evolution. In fact I was rather dismayed that some of the members of the Museum's scientific staff were anti-selectionists. They were also anti-Neo-Lamarckian and anti-Osbornian in their theoretical views.

I was not Neo-Lamarckian, as I was convinced that acquired characters are not inherited, and also that there is no *scala naturae*, which had been the other main Lamarckian principle but was not Neo-Lamarckian. I was also not a Neo-Darwinian in a strict sense of the term. Of course I knew that Darwin had considered the inheritance of acquired characters as a subsidiary factor in evolution, and that most evolutionary theorists before him, including Lamarck and Charles Darwin's grandfather Erasmus, and even some of my own contemporaries considered this a major or *the* major factor in evolution. It had by my time become clear that Darwin's hypothesis of how this occurred, even if it occurred, was flatly wrong. I did not believe that this occurred in any way, as the few remaining Neo-Lamarckians did. I also had learned while still in college that a whole new biological science of genetics had been developed since 1900.

Darwin also believed that what he called "sports" and geneticists were later calling mutations with large somatic effects might have some but probably a minor role in evolution. I was inclined to be dubious, but felt unable to decide. As all biologists now know, 1900 was the approximate date of what some geneticists did and do consider even now the "rediscovery" of Mendel's laws and thus of what they call Mendelism. Even before I wrote *Tempo and Mode in Evolution* I was somewhat put off by this. I did not doubt that the "laws," derived by Mendel from experimentation (perhaps with a little fiddling of his statistics) do apply to some aspects of inheritance in organisms. What I considered historically wrong was the opinion that Darwin was at fault in not being aware of these "laws," published in 1866, after the first edition of *The Origin of Species* (1859) but well before Darwin's last revision, the sixth, published in 1872. I also

was more than dubious about the direction taken by many geneticists after 1900. As this is involved in leading up to my writing of *Tempo and Mode in Evolution*, it requires at least brief further notice here.

The usual explanation of the tardiness of Darwin and other biologists to follow up Mendel's lead is that his crucial paper, in German, was not distributed widely enough for general notice. Such is not true. Mendel's paper was published in *Verhandlungen naturforschender Verein in Brünn* (Proceedings of the Naturalists' Union in Brünn). It was regularly distributed rather widely, and Mendel also distributed some copies. It would almost inevitably have interested any evolutionist especially interested in heredity, which Darwin surely was. There is no evidence one way or the other on whether Darwin did ever read or even hear of Mendel's paper. My point is that there was no particular reason why Darwin should have done so. Mendel made it clear that he was an anti-evolutionist, of which there were still all too many. To Mendel, his experiments showed how a population of a species could be quite variable but that species or crosses among subspecies or variants could be stable *without* evolving. Darwin's point was that species have evolved and that variants or subspecies can become species separate from their ancestry. That populations of species usually have evident variation was already well known to Darwin and clearly stated by him. Thus from Darwin's point of view, even if he had known of Mendel's conclusions, they would have been wrong on one main point and banal or superfluous on the other.

The "rediscoverers" of "Mendelism" were Hugo De Vries, Karl Erich Correns, and Erich Tschermak von Seysenegg. De Vries experimented with a species of evening primroses, *Oenothera lamarckiana*, and found that among them appeared characters strikingly different from those of either of their parent plants. He called these large and sudden genetic changes "mutations" and proposed a mutation theory of evolution on this basis. (Parenthetically I note that the word "mutation," meaning any sort of change, is old in English, having been used with a different spelling as early as Chaucer. It had also been used before De Vries in a technical sense by paleontologists for a perceptible change through geological time within an evolving lineage. Paleontologists have not used the word in that sense

since it has been taken over by the geneticists, who in the time of De Vries were unaware of the former paleontological usage.) According to De Vries' mutation theory evolution has been more effected by mutations, as he defined them (Darwin would have called them "sports"), than by the lesser variants of Darwinian theory. In that conception, the dominant process in evolution is chance mutation and not natural selection.

While I was still in graduate school it had been found, especially by O. Renner, that *Oenothera lamarckiana* is a peculiar organism and that its De Vriesian "mutations" comprise a mixture of different sorts of heredity likely to occur very rarely in nature. Then for a time geneticists thought (incorrectly as it has turned out) that all changes in heredity are of the same sort and can range from barely perceptible to Darwinian "sports" or De Vriesian "mutants." Nevertheless some continued to believe that mutation in that more general sense has been more effective in evolution than is natural selection, and that adaptation is largely by chance. When I joined the American Museum staff I was surprised to find that some very good zoologists, such as G. Kingsley Noble, a distinguished student of living amphibians, held that view.

In 1936 Harvard University celebrated its tercentenary with "a conference of arts and sciences," and I was invited to attend and to give an address. Although I was then 34 years old and had written more than 150 publications, this was my first strictly theoretical paper on an aspect of evolution as seen in the fossil record. I felt it rather daring of me. The paper was titled "Patterns of Phyletic Evolution" and was published in 1937 in the *Bulletin of the Geological Society of America*. In 1936 the American Society of Naturalists, with several other more specialized societies, held a symposium on "Super-specific Variation in Nature and in Classification" at a meeting with the American Society for the Advancement of Science. I read a paper on that subject "From the Point of View of Paleontology." The first part of this was based on studies of fossil mammals that I had collected in Patagonia (southern Argentina) and was then monographing, and the second part was a criticism of Kinsey's views based on his massive study of the wasp genus *Cynips*, then recently published. (Kinsey also contributed to the symposium; this was before his concentration on human sex.) My paper was published in *The*

American Naturalist in 1937. (I have been criticized, especially by Ernst Mayr, for not discussing the origin of species by cladistic separation of evolving populations in *Tempo and Mode in Evolution*.) In it, one of my earliest theoretical papers, I stressed and diagrammatically illustrated the fact that "super-specific" taxa necessarily arise on a basis of such speciation. You will find this also present in the book here reprinted.

In 1939 there was published a book on the application of statistical methods to living and fossil mammals, entitled *Quantitative Zoology* and jointly written with my childhood friend Anne Roe, who used statistical methods in her research in psychology, and who became my wife in 1938. In 1941, while I was writing the present book, I had published two theoretical papers and an abstract relevant to it: "The Role of the Individual in Evolution," "Quantum Effects in Evolution" (an abstract), and "Range as a Zoological Character." The latter was statistical, and it as well as *Quantitative Zoology* are relevant here because they represent the analysis and instrumentation of a concept of species and higher taxa as populations and not, as was long customary (and sometimes is held even now) as a sort of extended abstraction of taxa as individuals.

I have in a very summary way discussed some of the things that led up historically and in my own experience to the writing of the book here before you. Now I turn to the series of books on evolution in which this book first appeared.

Columbia Biological Series books published by Macmillan following the first, by Osborn, did not again deal with any particular approach, historical or otherwise, to evolution. The series was discontinued for a time, but it was taken up again, now published by Columbia University Press. The general editor for this revised series was Leslie Clarence Dunn (Dunny to his friends), a geneticist then a professor in the Department of Zoology at Columbia. Under his editorship four books on evolution were published from 1937 to 1950. The first, which was the eleventh in the series as a whole from 1894 on, was by Theodosius Dobzhansky (Dobie to his friends), another geneticist, then also a professor in the Department of Zoology at Columbia. This book was *Genetics and the Origin of Species*, published in 1937, with lightly revised new editions in 1941 and again in 1951. Second was *Systematics and the Origin of Species* by Ernst

Walter Mayr (Ernst to his friends), then associate curator of birds in the American Museum of Natural History. This was published in 1941 as thirteenth in the Biological Series. It was not followed by a revised edition as such. Third was by me (George to some friends, G to others) and was the book now before you as a reprint. It was first published in 1944 as the fifteenth book in the Biological Series. As will be noted later, it was followed in 1953 by a completely rewritten and retitled version, also published by Columbia University Press. The last of the four books devoted to evolution in the period here under consideration was *Variation and Evolution in Plants* by George Ledyard Stebbins, Jr. (Ledyard to his friends), a botanist and a professor of genetics at the University of California at Berkeley when he wrote the book. (He transferred to the campus at Davis the year it was published.) It was number sixteen in the Columbia Biological Series, published in 1950, and not followed by a revision as such.

In his introduction to the first of those four books, which was also the first of the resuscitated Series, Dunn wrote: "There was need for such a summary and synthesis of the new experimental evidence, and for reassessment of the older theories."

Although they had predecessors, it has been generally considered that these four books, considered together, established an approach to evolutionary theory that was and still is a synthesis as suggested by Dunn as editor. This approach has been generally known as a, or the, "synthetic theory," because it brings together and in a sense coordinates results of all the many specialized subspecies that bear on evolution. (Rather oddly, Dobzhansky mildly objected to the designation "synthetic" because he thought that some people might think of anything "synthetic" as artificial or not genuine!) Especially in Europe it is sometimes called "Neo-Darwinian" because it accepts Darwinian natural selection as a—not necessarily *the*—nonrandom feature of evolution. That designation is, however, historically and materially wrong. One has only to read Dobzhansky's own book in this series to see that the synthesis then already went far beyond and even contrary to Neo-Darwinism as so designated in the late nineteenth century.

It is unnecessary here to say why I wrote *Tempo and Mode in Evolution* because I think that is made perfectly clear in the original

introduction, also reprinted here. The way in which I approached this task is perhaps not quite so clear there, but is evident throughout the book. It will also be evident that I had studied and profited by Dobzhansky's *Genetics and the Origin of Species*, the first edition of which was published not long before I started to write this book and the second (first revised) edition while I was writing it. It is apparent also that when I wrote I had not read Mayr's *Systematics and the Origin of Species*. That was published before *Tempo and Mode in Evolution* but after I had finished writing it and at a time when I could not study, and in fact could not obtain, a copy of Mayr's book.

This book has sometimes been dismissed as devoted only to the proposition that paleontology is not contradictory to genetics as genetics was at the time I wrote. That was one of my aims, but I do not see how anyone who has really read this book could fail to understand that it was not my only or even my main aim. My main aim was to explore and in a way to exploit the fact that paleontology is the only four-dimensional biological science: time, "tempo," is inherent in it. Thus the aim of this book, which I think it accomplished, was to bring this dimension squarely, methodologically, into the study of evolutionary theory.

The pre-Darwinian English classics of creationism were the Bridgewater Treatises and Paley's "Natural Theology." These emphasized the obvious fact that all organisms are adapted to live where, when, and how they do live. Their conclusion was that this can be explained only by a Creator following up a divine plan. The problem and the strategy for Darwin was therefore to find some way in which evolution, without divine creation as such, could produce the observed results of adaptation. He found it in natural selection. From 1900 on the followers of the new science of genetics had tended to oppose the theory of natural selection. Although he had forerunners, whom he cited, Dobzhansky's book in this series both by field and by laboratory studies established the recognition that natural selection can and does produce adaptive evolution.

In the book here present I adopted that theory and exemplified it as a process occurring in the time dimension. In this respect it will also be noted that I discussed the views of Goldschmidt, an able naturalist and in an odd way a geneticist who did not think in terms

of genes. He maintained that marked adaptive changes in evolution occurred not by natural selection in the course of generations but by the chance production of "hopeful monsters" by what he called "systemic mutation," instantaneous remodeling of the whole genetic system. Early in the present century some able paleontologists, notably William Diller Matthew (1871–1930) also found evidence for natural selection in the fossil record. However in 1936 another able paleontologist had attempted to reconcile the different views of early geneticists with those of paleontologists but had come to a conclusion quite like Goldschmidt's although different in detail or mechanism. In the present book I opposed both Goldschmidtian genetics and Schindewolfian paleontology for reasons fairly clear in the following pages.

Between 1944 and 1953 I found myself a *homo unius libri*, in spite of my book *The Meaning of Evolution* having been published by Yale University Press in 1949. However, that book was meant to be, and was, a popular book, widely read and translated into many languages but rarely noticed by my more technical colleagues. Also in 1949 was published by Princeton University Press a symposial volume, *Genetics, Paleontology, and Evolution*, edited by Glenn Jepsen, me, and Ernst Mayr, with a foreword by Jepsen and chapters by me and by Mayr. This was oriented by the synthetic theory, which was also having wide influence internationally on all students of evolutionary theory. By 1951 so much more had been done in this field that, as I remarked, "*Tempo and Mode in Evolution* [had] helped to produce its own obsolescence," and that "[It] had served its purpose and should be allowed to fossilize quietly." However Columbia University Press said it was not dead enough for that and wanted it to be revised instead. I revised it so thoroughly that although it followed the plan of *Tempo and Mode* it was completely rewritten and considerably lengthened (from 237 to 434 pages). The manuscript was completed at the end of 1951 but editing, indexing, proofreading, and manufacture carried publication by Columbia University Press into 1953.

Because of the changes, additions, and rewriting that book was given a different title, *Major Features of Evolution*. In general I continued to be *homo unius libri*. In my case the one book cited continued to be *Tempo and Mode* in some studies by others, but more

commonly it has been *Major Features*. One or two evolutionists who had welcomed *Tempo and Mode* as a good pioneering try nevertheless have condemned *Major Features* as not equally pioneering and even as being an effort to fix a dogma, which indeed is not true as those who have read and understood it have usually recognized. Some whose attention was on speciation and minor features of evolution have also failed to appreciate that the intention of the book was to elucidate *major* features, which it did.

In this thorough revision I had finally at hand Mayr's book in the Columbia Biological Series, the second revision (third edition) of Dobzhansky's book in the series, and Stebbins' book in the series. There were also a large number of other relevant new studies, almost all in the general trend of the synthetic theory more or less as set out in the four books of the series including *Tempo and Mode* on the paleontological side. An early exception was Schindewolf, who in 1950 had published two more works continuing his view that his paleontological data supported evolution by "mutations" like those of De Vries or like Goldschmidt's "systemic mutations." In *Major Features* somewhat more adverse critical attention was therefore given to Schindewolf's views. It may interest the reader that Schindewolf subsequently visited the United States and the American Museum of Natural History, where I was then working, and that he carefully avoided me. It is also of interest that in 1958 Marjorie Grene, a classical philosopher, without firsthand knowledge of paleontology or genetics, wrote a long study of "Two Evolutionary Theories," mine and Schindewolf's. She decided in favor of Schindewolf mainly on the grounds that his view was closer than mine to those of the ancient Greeks. Francisco Ayala, who is the unusual combination of being a well-trained and active student both in philosophy and in evolutionary genetics, has demolished Grene's arguments on this subject, both philosophical and biological.

Before writing *Major Features* and thus in a sense rewriting *Tempo and Mode* I had also gone on with relevant theoretical studies as well as adding significantly to knowledge of the fossil record. Among other publications may be mentioned "The Problem of Plan and Purpose in Nature" (1947, in *The Scientific Monthly*), "Rates of Evolution in Animals" (a chapter in the 1949 book edited by Jepsen, me, and Mayr, noted above), a revision of *The Meaning of Evolution* (1967), "Evo-

lutionary Determinism and the Fossil Record" (1950, in *The Scientific Monthly*), "Periodicity in Vertebrate Evolution" (1952, in *Journal of Paleontology*) and, among books, *This View of Life* (Harcourt, Brace and World, 1964).

All of the authors of what may be fairly considered the four classics of synthetic theory in the Columbia University Biological Series went on to expand and update their own views and also to bring other branches of science into the synthesis. Among Dobzhansky's later books is *Genetics of the Evolutionary Process* (Columbia University Press, 1970). Among Mayr's is *Animal Species and Evolution* (Belknap Press of Harvard University Press, 1963). Among mine the most recent is *Fossils and the History of Life* (W. H. Freeman/Scientific American, 1983). Among Stebbins' is *Processes of Organic Evolution* (Prentice-Hall, 1966). As an example of integration with other branches there is *Behavior and Evolution*, edited and with chapters by Anne Roe and me (Yale University Press, 1958).

The synthetic theory of evolution has never been supported as dogmatic or as an acceptable a priori approach to evolution in any publication that I know of. Knowledge is constantly advancing in all the relevant sciences, from molecular biology to ethology, to name two specialties with little in common except through evolutionary theory. The synthetic theory thus becomes more complex and modified in detail as time goes on, but it has not been clearly and indubitably contradicted as indeed a synthesis of everything known about evolution at a given time. So positive a statement requires brief notice of what does claim to be a "new and general evolutionary theory" which nominally rejects the synthetic theory. This is called "punctuated equilibrium," and the synthetic theory is condemned as "gradualistic." By "punctuation" is meant essentially what is meant by "quantum evolution" in *Tempo and Mode in Evolution*, the origin of a species or other taxon by exceptionally rapid evolution. In his first statement Gould called this "the Goldschmidt break," and he suggested that speciation may involve Goldschmidtian "rapid reorganization of the genome, perhaps non-adaptive." By "equilibrium" he meant that after the "Goldschmidt break" species usually do not change further for a considerable length of geological time. More recently Gould has essentially abandoned the "Goldschmidt" break and has redefined "punctuation" as being continuous but so

break and has redefined "punctuation" as being continuous but so rapid as to seem practically instantaneous in stratigraphic observation. He also has urged to take as given the fossil record, in which species and other taxa often, but not invariably, do appear rapidly or even "instantly," that is, in a span of geological time so short as not to have been measured. As all paleontologists have always known, the incompleteness of the fossil record is factual and is the most logical explanation of apparent "quantum evolution" or "punctuation." New species are still being found and named every day so the record becomes more and more reliable, but it is also obvious that fossils representing every species that ever lived do not now exist; thus, rich as the known record is becoming, it can never be literally complete. Nevertheless, as in *Tempo and Mode* and later studies, the fossil record does provide a factual basis for evolutionary theory.

Gould lumped together Darwinism, Neo-Darwinism, and Synthesis as "gradualism." As he defined "gradualism," it was a straw man for his attack. That term is not a description of any of the schools of thought that he wants to reject. "Gradualism" *sensu* Gould is one end of a continuum and "punctuated equilibrium" is the other end. We thus have here an "either-or" proposition, a Hegelian or Marxian dialectic. It is apt to point out that apparent contradiction between *thesis* and *antithesis* leads logically not to one or the other but to *synthesis*. That is what the synthetic theory does.

In closing it may be pointed out that the book you are about to read has been read by almost everyone who has been involved in the study of evolution since 1944. It has been widely circulated not only in English but also in French, German, and Russian.

G. G. Simpson

Introduction

THE BASIC PROBLEMS of evolution are so broad that they cannot hopefully be attacked from the point of view of a single scientific discipline. Synthesis has become both more necessary and more difficult as evolutionary studies have become more diffuse and more specialized. Knowing more and more about less and less may mean that relationships are lost and that the grand pattern and great processes of life are overlooked. The topics treated in the present study do not embrace the whole subject of evolution, but they are fundamental in nature and broad in scope. They are among the basic evolutionary phenomena that have tended to be obscured by increasing specialization and that overlap many different fields of research. Data and theories from paleontology, genetics, neozoology, zoogeography, ecology, and several other specialties are all pertinent to these themes. The complete impossibility of attaining equal competence and authority in all these fields entails unavoidable shortcomings, but the effort to achieve such a synthesis is so manifestly desirable that no apology is in order. The intention will hardly be criticized, whatever is said about its execution.

The attempted synthesis of paleontology and genetics, an essential part of the present study, may be particularly surprising and possibly hazardous. Not long ago paleontologists felt that a geneticist was a person who shut himself in a room, pulled down the shades, watched small flies disporting themselves in milk bottles, and thought that he was studying nature. A pursuit so removed from the realities of life, they said, had no significance for the true biologist. On the other hand, the geneticists said that paleontology had no further contributions to make to biology, that its only point had been the completed demonstration of the truth of evolution, and that it was a subject too purely descriptive to merit the name "science." The paleontologist, they believed, is like a man who undertakes to study the principles of the internal combustion engine by standing on a street corner and watching the motor cars whiz by.

Now paleontologists and geneticists are learning tolerance for each other, if not understanding. As a paleontologist, I confess to inadequate knowledge of genetics, and I have not met a geneticist who has demonstrated much grasp of my subject; but at least we have come to

realize that we do have problems in common and to hope that difficulties encountered in each separate type of research may be resolved or alleviated by the discoveries of the other.

Earlier work in genetics was devoted mainly to studying the transmission of inherited characters, cryptogenetics. Earlier work in paleontology was devoted largely to the determination of the forms and sequence of fossil animals and to their classification. There is hardly any point of contact between these subjects, and it is not surprising that workers in the two fields viewed each other with distrust and sometimes with the scorn of ignorance. Now this basic work in both subjects, although far from completed in either, is so well advanced that what remains must in great part follow charted paths. Both geneticists and paleontologists are turning to new fields. In genetics the vigorous and trail-blazing work is now more likely to be in the field of phenogenetics—not how heredity occurs, but how hereditary characters achieve their material expression in the life cycle of an animal or plant and in the third major division of modern genetics, that of population genetics.

In paleontology there is fresh interest in attempting to infer not only the course but also the mechanisms of evolution. This is not new, to be sure, for even the earliest paleontologists did speculate as to causes, just as the early experimentalists did pay some attention to natural populations; but the attack is now being made with more hope and with better techniques. The paleontologist is acquiring a different attitude toward variation, which was only a nuisance to the classifier, but is now becoming an important study in itself and one that is improving greatly in method. Like the geneticist, the paleontologist is learning to think in terms of populations rather than of individuals and is beginning to work on the meaning of changes in populations. Thus, from very different starting points geneticists and paleontologists have come to the study of problems that are not only related but also sometimes identical.

For the study of these problems it is the great defect of paleontology that it cannot directly determine any of the cryptogenetic factors that must, after all, be instrumental in the evolution of populations. Fossil animals cannot be brought into the laboratory for the experimental determination of their genetic constitutions. The experiments have been done by nature without controls and under conditions too com-

plex and variable for sure and simple analysis. The paleontologist is given only phenotypes, and attempts to relate these to genotypes have so far had little success. But here genetics can provide him with the essential facts. One cannot directly study heredity in fossils, but one can assume that some, if not all, of its mechanisms were the same as those revealed by recent organisms in the laboratory. One cannot identify any particular set of alleles in fossils, but one can recognize phenomena that are comparable with those caused by alleles under experimental conditions.

On the other hand, experimental biology in general and genetics in particular have the grave defect that they cannot reproduce the vast and complex horizontal extent of the natural environment and, particularly, the immense span of time in which population changes really occur. They may reveal what happens to a hundred rats in the course of ten years under fixed and simple conditions, but not what happened to a billion rats in the course of ten million years under the fluctuating conditions of earth history. Obviously, the latter problem is much more important. The work of geneticists on phenogenetics and still more on population genetics is almost meaningless unless it does have a bearing in this broader scene. Some students, not particularly paleontologists, conclude that it does not, that the phenomena revealed by experimental studies are relatively insignificant in evolution as a whole, that major problems cannot now be studied at all in the laboratory, and that macro-evolution differs qualitatively as well as quantitatively from the micro-evolution of the experimentalist. Here the geneticist must turn to the paleontologist, for only the paleontologist can hope to learn whether the principles determined in the laboratory are indeed valid in the larger field, whether additional principles must be invoked and, if so, what they are.

On two topics, in particular, the paleontologist enjoys special advantages. It is with reference to these topics that the geneticist and the general student of evolution now turn most frequently to paleontology for enlightenment and too often turn in vain. The first of these general topics has to do with evolutionary rates under natural conditions, the measurement and interpretation of rates, their acceleration and deceleration, the conditions of exceptionally slow or rapid evolutions, and phenomena suggestive of inertia and momentum. In the present study all these problems are meant to be suggested by the

word "tempo." The group of related problems implied by the word "mode" involves the study of the way, manner, or pattern of evolution, a study in which tempo is a basic factor, but which embraces considerably more than tempo. The purpose is to determine how populations became genetically and morphologically differentiated, to see how they passed from one way of living to another or failed to do so, to examine the figurative outline of the stream of life and the circumstances surrounding each characteristic element in that pattern.

Readers have been led to expect that a study of evolution by a paleontologist will have as its subject matter, first, descriptions of the morphology and phylogeny of particular lines of extinct animals and, second, discussion of some empirical principles of morphogenesis such as convergence, irreversibility, or polyisomerism. The reader is warned at the outset that this study mentions neither of these subjects except incidentally. Phylogenetic examples are introduced as evidence and to give reality to the theoretical discussion, but they are not expounded in detail or as an end in themselves. Some of the so-called paleontological laws of morphogenesis are mentioned, but only as they bear on the broader problems of tempo and mode. Phylogeny and morphogenesis continue to be chief aims of paleontological research, but the present purpose is to discuss the "how" and—as nearly as the mystery can be approached—the "why" of evolution, not the "what." This is now a more stimulating point of view for the paleontologist, one more suggestive of new lines of study, and it is more immediately interesting to the nonpaleontological evolutionist who wishes to have the evidence interpreted in ways more directly applicable to his own problems.

For almost every topic discussed in the following pages the data are insufficient. The student who attempts interpretations under these circumstances does so in the face of certainty that some of his conclusions will be rejected. It is, however, pusillanimous to avoid making our best efforts today because they may appear inadequate tomorrow. Indeed, there would be no tomorrow for science if this common attitude were universal. Facts are useless to science unless they are understood. They are to be understood only by theoretical interpretation. The data will never be complete, and their useful, systematic acquisition is dependent upon the interpretation of the incomplete data already in hand. The one merit that is claimed for this study is that it suggests new ways of looking at facts and new sorts of fact to look for.

Tempo and Mode in Evolution

Chapter I: Rates of Evolution

HOW FAST, as a matter of fact, do animals evolve in nature? That is the fundamental observational problem of tempo in evolution. It is the first question that the geneticist asks the paleontologist. Some attempt to answer it is a necessary preliminary for the whole consideration of tempo and mode. Answers can be given, not general answers, but those derived from studies of rates in a few typical cases. These answers are useful, they are suggestive of broader fields for study, and they will serve to supply concrete examples for reference throughout this work. Yet they are not fully satisfactory, because here at the very beginning the study of evolutionary tempo comes up against the gravest sorts of difficulty. There have been many sporadic enquiries, but there has been no systematic accumulation of the needed data. More fundamentally, the concept of rate of evolution is complex and involves many inherent impediments, as will be seen.

Rate of evolution might most desirably be defined as amount of genetic change in a population per year, century, or other unit of absolute time. This definition is, however, unusable in practice. Direct study of genetic change is impossible to the paleontologist. It is, so far, possible only to a limited extent among living animals, and these usually do not change sufficiently in the time available to yield a reliable measure of rate. Even rough estimation has some usefulness, but absolute time cannot yet be accurately measured for paleontological materials, and it is desirable to examine relative as well as absolute rates.

For present purposes, then, rate of evolution is practically defined as amount of morphological change relative to a standard. It is assumed that phenotypic evolution implies genetic change and that rates of evolution as here defined are similar to, although not identical with, rates of genetic modification. This morphological approach to these particular problems is logical, because it is the organism, the phenotype, as an agent in an evolving world with which we are directly concerned. The implicit genetic factors are important less for their own sake than because they are determinants of phenotypic evolution.

The morphological changes studied may be in a single zoological character, giving a unit character rate, or in a number of related char-

acters, a character complex rate, or in whole animals, an organism rate. They may be followed in single lines of descent, a phyletic rate, or averaged over a larger taxonomic unit, a group rate. The scale of comparison or rate division may be absolute time, giving an absolute rate, or an external variate correlated with time, a correlative rate, or an associated change within the group studied, a relative rate. Paleontological data will be adduced to exemplify each of these different kinds of evolutionary rate.

RELATIVE RATES IN GENETICALLY RELATED UNIT CHARACTERS

In any phyletic series various different characters are changing over the same period of time. Paleontologists have long noticed that two such characters may evolve in such a way that the direction and rate of change in one are functions of the change in the other. Various theories of orthogenesis, purposive evolution, and the like have been based on such observations. The methods of analysis of relative growth, largely developed and summarized by Huxley (1932), have cast unexpected light on these phenomena. It has been found that the varying relative sizes of different structures are frequently determined by a constant relationship of their growth rates. This suggests that changes in proportions in evolution may be determined in the same way.¹ Paleontological study along these lines has barely begun, but it already amply demonstrates that this is true in many cases.

It is well known that the sequence from *Hyracotherium* to *Equus* involves increase in gross size and accompanying increase in the length of the muzzle relative to the cranium. Robb (1935) has expressed and studied this phenomenon of "progressive pre-optic predominance" in terms of relative growth. His work shows that the absolute rates of increase of the muzzle length and of the total skull length are different, but that they tend to maintain a constant ratio to each other—that is, that the relative growth of these two parts tends to be constant. The relationship can be approximately expressed by the equation $Y = .25 X^{1.23}$, in which Y is the preorbital length, X the skull length, and 1.23 the ratio of the rate of increase in Y to that in X . Practically the same equation applies not only (1) to successive stages in a single

¹ Not because of any direct analogy between ontogeny and phylogeny, but because the structure of every adult individual in the evolutionary series is the result of its ontogeny, and ontogeny is hereditary.

phyletic sequence leading to *Equus* but also (2) to contemporaneous equid races of different sizes and (3) to the ontogenetic development of *Equus caballus* (see Fig. 1). It has not been demonstrated in this case, but is a corollary of these demonstrations and is known to be

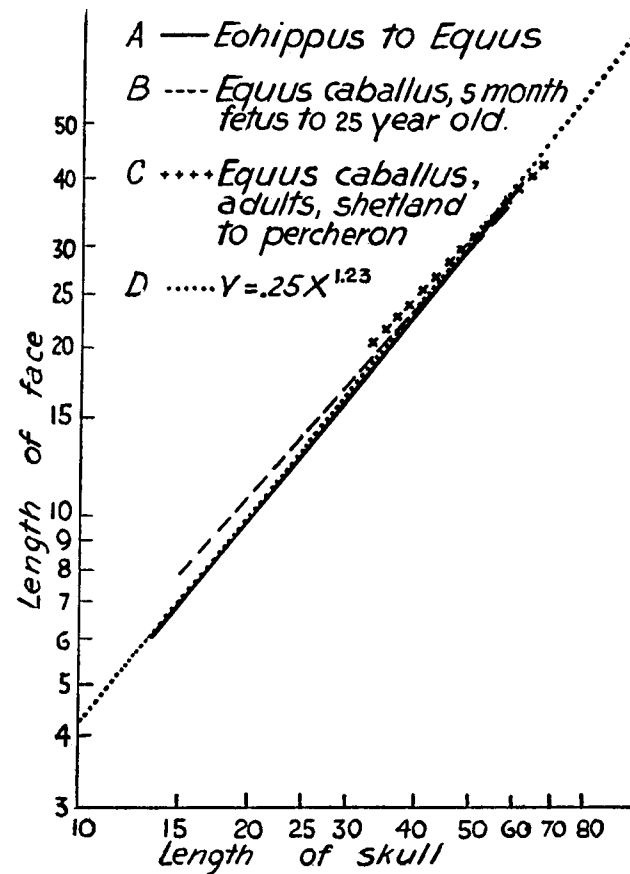


FIG. 1.—Relative rates in horses. Double logarithmic graph of regression of length of face on length of skull, Robb's data: A, phylogeny in the line *Hyracotherium-Equus*; B, Ontogeny in *Equus caballus*; C, races of *Equus caballus*, adults; D, heterogony formula nearly fitting all three observed regressions. (Lines A-C fitted by eye.)

true in numerous analogous cases, that the same relationship holds true (4) between adults of different sizes belonging to a single race.

These data make it so probable that it amounts almost to a proven fact that the relative sizes of the two variates in question are genet-

ically related or have proportions resulting from a single genetic rate determinant. In the horse skull there was no evolution of this character, which seems to have been constant throughout the whole family for some 45 million years. The striking changes in skull proportions were only the result of the sizes reached by adults of the various species, and evolution in the size of the average adult did occur.

Subsequent similar work by Robb (1936) on the proportions of the digits in the horse foot revealed a still more significant set of phenomena. In three-toed horses the length of either side toe (digits II and IV) is a relatively simple function of the length of the cannon bone (metapodial of III): $Y = 1.5 X^{.97 \text{ to } .98}$, in which Y is the total length of either lateral digit and X the length of the cannon bone of the same foot. This is similar to the previous result for skull proportions, except that the heterogeneity is negative and less in degree—indeed, it is not established that the heterogeneity is significant. The side toes maintained nearly or quite a constant ratio to the cannon bone. The reduction is not surely progressive, as has been universally stated, and the side toes nearly retained the ancestral proportions as long as they were functional at all. But in the one-toed horses the relationship of splints to cannon bone is abruptly different: $Y = .76 X^{.99 \text{ to } 1.00}$.

The constant b (of the formula $Y = bX^k$) is only one-half as large, while k is about the same. Thus, the change from three-toed to one-toed is not simply related to size or to foot elongation, but involves a particular genetic change or mutation, related to this character as a separate entity. In a later paper (1937) Robb shows that this relationship is essentially the same in recent horse ontogeny and between recent horses of different sizes: $Y = .75 X^{.99}$. Thus unlike skull proportions, digit proportions did evolve, in themselves, but they did so only in one stage of horse evolution and as far as has yet been observed, in one step.

Phleger (1940) and Phleger and Putnam (1942) have made extensive studies on relative growth rates in felids and oreodonts. In these groups they found marked differences in homologous rates in related species and genera, demonstrating evolution and differentiation more extensive than that in the two rates studied by Robb. Phleger's data also hint, although they are insufficient to prove, that different relative growth rates may occur within one population, as if they were the expression of alleles.

In such cases—and they will surely be found to include many of the characters used in the paleontological study of evolution—the impression as to rates of evolution derived from simple observation of morphology may be seriously misleading. Study of the evolution of equid preorbital dominance is a study of a character that did not evolve genetically but only morphologically. In the study of similar proportions in oreodonts, inspection of individuals cannot determine whether genetic evolution has occurred or not unless, as is rarely true, skulls of exactly the same size are available in successive stages. The true rate of evolution in these examples is the rate of change in regression, not that of change of proportion in adults, which is the resultant of regression and of mean adult size.

The criteria for recognition of this situation are that the regression tends to be the same within individuals, between individuals of one population, and also, except as modified by a recognizable mutational advance, between related contemporaneous populations and between ancestral and descendent successive populations. With paleontological materials the intraindividual regression is not available, but an analogous test may be made by comparing the regression of growth stages with that between individuals in a single growth stage and both of these with regressions between distinct contemporaneous and successive populations. It is not true that all relative rates of evolution are determined by a single growth factor governing the development of the two or more characters involved, as will appear from the next example.

RELATIVE AND ABSOLUTE RATES IN GENETICALLY INDEPENDENT CHARACTERS

Another striking progressive character in the evolution of the horse is hypsodonty, increase in height of cheek tooth crowns relative to their horizontal dimensions. The situation here is more complex than in the examples of relative evolutionary rates studied by Robb, Phleger, and Putnam. Both vertical and horizontal dimensions of these teeth are positively correlated with gross size of the animal (and hence with almost all its other linear dimensions) in all three of the possible ways: within populations, between contemporaneous populations, and between successive populations. These tooth characters have no genetically controlled intra-individual variation. Hypsodonty, the relation-

ship between vertical and horizontal dimensions, is positively correlated with size and with most linear dimensions among successive populations, but shows no such correlations among individuals or among contemporaneous populations.² The successive intergroup correlation is thus spurious, like so many correlations between temporal sequences. Hypsodonty and size both developed progressively but did so independently. The horses became larger and more hypsodont, but the two characters are separately determined in a genetic sense. Any real relationship was indirect and nongenetic, for instance through natural selection because greater hypsodonty assists the survival of larger animals.

Hypsodonty is one of the most important elements in horse evolution (with size, coronal pattern, and foot structure), but there are few good data on it. For the present illustrative purposes five small samples have been selected from the American Museum collections and the essential data gathered and analyzed. Among many possible measures of hypsodonty, the following index was selected as best adapted to the available material: $100 \times (\text{paracone height}) / (\text{ectoloph length})$.

Measurements were made on unworn M³. The samples have the following identifications and specifications:

Hyracotherium borealis: Lower Eocene, Graybull Formation, Bighorn Basin, Wyoming

Mesohippus bairdi: Middle Oligocene, Lower Brulé Formation, Big Badlands, South Dakota

Merychippus paniensis: Upper Miocene, associated in a "Lower Snake Creek" deposit, Nebraska

Neohipparion occidentale: Late Lower or Early Middle Pliocene, associated in an "Upper Snake Creek" deposit, Nebraska

Hypohippus osborni: Upper Miocene, associated in a "Lower Snake Creek" deposit, Nebraska

Hyracotherium-Mesohippus-Merychippus-Neohipparion and *Hyracotherium-Mesohippus-Hypohippus* represent approximate genetic phyla. *Neohipparion* and *Hypohippus* are thus typical of divergent phyla of common ancestry (slightly beyond the *Mesohippus* stage).

² This statement agrees with, but is not proven by, calculated correlation coefficients. Hypsodonty can only be measured as a ratio, and the statistical correlation of a ratio with one of its elements or with a variate correlated with the latter is frequently spurious. Nevertheless, the stated independence is an evident and, I believe, incontrovertible biological fact.

Some of the pertinent statistics³ are given in Table 1:

TABLE 1

MEASUREMENTS ON M³ OF FIVE SAMPLES OF FOSSIL HORSES

A. PARACONE HEIGHT IN MILLIMETERS					
	N ^a	O.R.	S.R.(S.D.)	M	σ
<i>Hyracotherium borealis</i>	11	4.2- 5.1	1.9	4.67 ± 0.09	0.29 ± 0.06
<i>Mesohippus bairdi</i>	14	7.8- 9.4	2.6	8.36 ± 0.11	0.40 ± 0.08
<i>Merychippus paniensis</i>	13	29.6-37.6	13.0	34.08 ± 0.56	2.01 ± 0.39
<i>Neohipparion occidentale</i>	5	49-55	15.6	52.40 ± 1.08	2.41 ± 0.76
<i>Hypohippus osborni</i>	4	16.7-22.4	17.0	18.75 ± 1.31	2.62 ± 0.93
B. ECTOLOPH LENGTH IN MILLIMETERS					
	N ^a	O.R.	S.R.(S.D.)	M	σ
<i>Hyracotherium borealis</i>	11	7.6- 8.9	3.0	8.21 ± 0.14	0.46 ± 0.10
<i>Mesohippus bairdi</i>	14	11.0-13.0	3.6	11.89 ± 0.15	0.55 ± 0.10
<i>Merychippus paniensis</i>	13	17.7-21.7	6.9	19.96 ± 0.29	1.06 ± 0.21
<i>Neohipparion occidentale</i>	5	19-22	7.1	20.80 ± 0.49	1.10 ± 0.35
<i>Hypohippus osborni</i>	4	19.4-26.4	20.5	22.03 ± 1.59	3.17 ± 1.12
C. 100 × A/B					
	N ^a	O.R.	S.R.(S.D.)	M	σ
<i>Hyracotherium borealis</i>	11	54-60	11.7	57.0 ± 0.5	1.8 ± 0.4
<i>Mesohippus bairdi</i>	14	64-77	20.7	70.4 ± 0.9	3.2 ± 0.6
<i>Merychippus paniensis</i>	13	155-184	48.0	170.7 ± 2.1	7.4 ± 1.5
<i>Neohipparion occidentale</i>	5	241-262	61.6	252.2 ± 4.3	9.5 ± 3.0
<i>Hypohippus osborni</i>	4	84-88	11.0	85.5 ± 0.9	1.7 ± 0.6

^a N, size of sample; O.R., observed range (by extreme measurements); S.R.(S.D.), standard range from standard deviation (by span); M, mean; σ, standard deviation. The last two with standard errors.

The same data are graphically shown in Fig. 2, set up to represent the hypothesis that the (geometric) growth rate of ectoloph length was constant (by placing these values in a straight line on semilog coordinates). The assumption that gross size increase (with which ectoloph length is closely correlated) was approximately constant in rate has been made for this and other so-called orthogenetic series. The diagram shows, in fact, that the hypothesis is false, for if it were true the horizontal distances between species would be proportionate to the geologic ages, whereas *Hypohippus osborni* comes out much too far to the right, the distance from *Neohipparion occidentale* to *Merychippus paniensis* is surely too small, and that from the latter species to *Mesohippus bairdi* is probably too large, relative to the *Hyracotherium-Mesohippus* distance. The more important conclusion from the diagram is, however, that the rate of evolution of height behaved in a very different way from that of ectoloph length. Plotting these as for

³ Here and elsewhere, it is assumed that the reader is familiar with elementary statistics. For an introduction to this subject, see Simpson & Roe (1939).

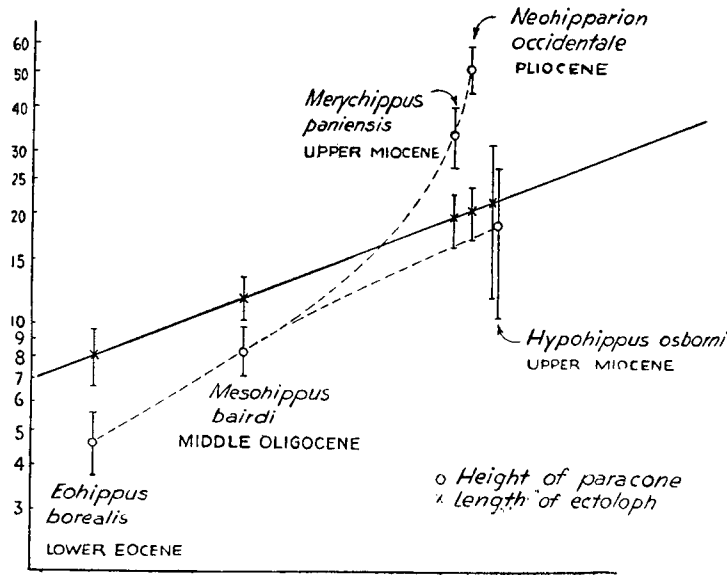


FIG. 2.—Relationships of structural changes in two characters of five genera of Equidae. Height of unworn paracone and length of ectoloph of M^3 , data in text. Ordinate scale logarithmic, no abscissal scale; arranged in hypothesis of rectilinear mean increase in ectoloph length. Circles and crosses are means of samples. Vertical lines are standard ranges, statistical estimates of variation in a population of 1,000 individuals.

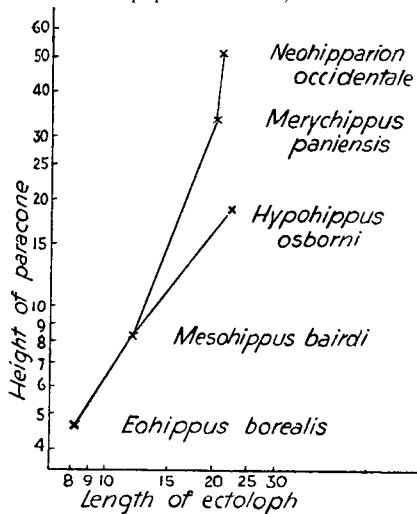


FIG. 3.—Relative rates of evolution in equid molars. Same data as for Fig. 2 (means of samples only) with paracone height plotted against ectoloph length on double logarithmic co-ordinates.

relative growth (Fig. 3), it is seen that the rate for paracone height was higher than for ectoloph length throughout, that the ratio of these rates was approximately constant in the *Hyracotherium-Hypohippus* line, but that the rate for paracone height showed differential acceleration in the *Mesohippus-Neohipparion* line.

In Fig. 4 an attempt is made to show the true temporal trends in these rates. The plot is semilog, with time on the arithmetic scale. The

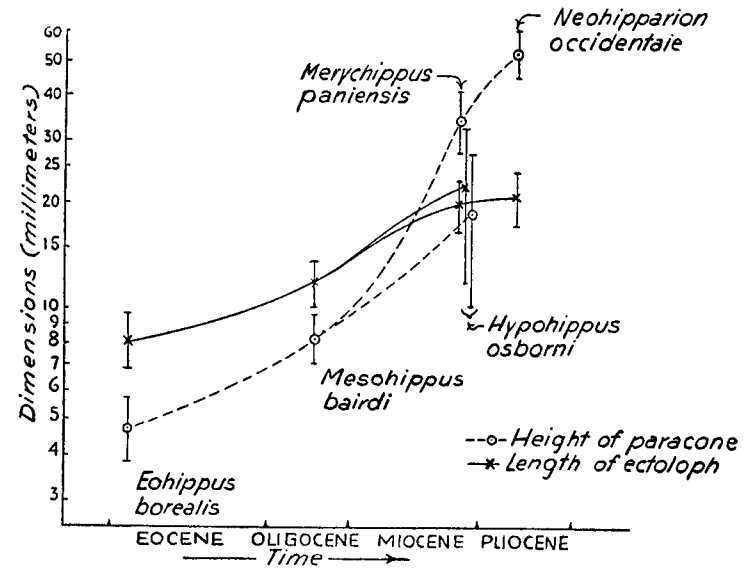


FIG. 4.—Phylogeny of five genera of Equidae and evolution of two related tooth characters. Data as for Fig. 2. Ordinate scale, logarithmic, absolute dimensions. Abscissal scale, arithmetic, approximation of absolute lapse of time (probable relative lengths of epochs represented in arithmetic proportion). Slopes of lines are proportionate to rates of evolution of the unit characters.

precise absolute or relative lengths of the Tertiary epochs are unknown, but the relative lengths were probably more or less as shown. It is seen that neither rate was constant in the two phyletic series involved. Both show acceleration toward the end of the Oligocene. The acceleration in increase of paracone height was greater and continued until about the Middle Miocene. Both show deceleration in the Late Miocene; this is more pronounced in ectoloph length, so that increase of this dimension almost ceases in the Pliocene. The rate is more nearly constant for ectoloph length than for paracone height. For ectoloph

length the rates in the two phyla diverge very little—the data are insufficient to prove that the small apparent divergence is not due to chance. For paracone height, however, the rates in the two phyla diverge markedly and significantly. In the Miocene this dimension increased much more rapidly in the line leading to *Neohipparion* than in that leading to *Hypohippus*. The result is that *Hypohippus*, although decidedly more hypsodont than the common ancestry of the two lines, is much less hypsodont than the contemporary *Merychippus*.

Hypsodonty is a single character from a physiological point of view and it is unquestionably a unit in its reaction with the pressure of natural selection; but it here appears as a resultant of two other and simpler characters evolving with considerable, not complete, independence from each other. The probable reasons for the slow advance of hypsodonty throughout and its marked acceleration in one line during the Miocene will be discussed in a later section.

Study of the other essential differences between *Merychippus* and *Hypohippus* shows that most of them arose because of differences in rates of evolution, both the rates and the differences between them being distinctive for each character. This is a widespread evolutionary phenomenon in diverging phyla of abundant animals evolving at moderate rates.

The Equidae are thus found to illustrate four basic theorems concerning rates of evolution:

1. The rate of evolution of one character may be a function of another character and not genetically separable even though the rates are not equal.

2. The rate of evolution of any character or combination of characters may change markedly at any time in phyletic evolution, even though the direction of evolution remain the same.

3. The rates of evolution of two or more characters within a single phylum may change independently.

4. Two phyla of common ancestry may become differentiated by differences in rates of evolution of different characters, without any marked qualitative differences or differences in direction of evolution.

CORRELATIVE RATES

A correlative rate can be determined when the values of a morphological variate are correlated with some variate external to the animals

and the latter variate is, in turn, correlated with time. The usual external variate is thickness of strata, and rates relative to such thicknesses have frequently been used, especially for marine invertebrates. That the stratigraphic succession is temporal, when correctly determined, is a proven fact, but the validity of the method also demands a constant relationship between not only succession but also thickness of strata and time, that the rate of deposition shall have been approximately constant. This is difficult to prove and frequently is not true, so that the usefulness of the method is sharply limited. Moreover, the usual proof of sedimentary continuity is faunal continuity, and then the determination of rates of evolution relative to sedimentary units is invalid. Nevertheless, the method can give some information about fluctuations in rates of evolution, and it is a valid way of comparing the rates of different characters or of different phyla during the same span of time (identical sequences of strata).

Demonstration that a character has significantly evolved in a given series of strata may be made, among other ways, by calculation of a correlation coefficient or by analysis of variance into intersample and intrasample, the samples being successive. These figures do not measure any rate of evolution, however, and of several possible measures of rate probably the most useful is the regression coefficient in cases of nearly rectilinear regression against thickness of strata.

One of the most extensive and completely analyzed sets of data from which correlative rates can be obtained was given by Brinkmann (1929) for the ammonite genus *Kosmoceras* through about 13 meters of predominantly fine-grained sediments near Peterborough, England. Table 2 presents typical data, rearranged and somewhat revaluated, from statistics calculated by Brinkmann.

Only for the groups of strata in which the correlation coefficient is significant do the data demonstrate that any change in the character took place (i.e., that either the correlation coefficient or the regression coefficient is likely to exceed zero). The value of such subdivided data is that they reveal that rates have changed, not simply that evolution did occur or what its average value is over a long span. In dealing with a single character, comparisons are valid only if no hiatus is present within any one class of the stratigraphic sequence. This is not apparent from the table itself, but other information in Brinkmann's paper shows that there is no significant hiatus within this table.

TABLE 2

CORRELATION AND REGRESSION WITH THICKNESS OF STRATA FOR TWO CHARACTERS OF *Kosmoceras* (*Zugokosmoceras*)

Character	Strata Distance in cm. from bottom of section.	N ^a	r	b
I Terminal diameter	b. 26-28	23	.32	3.0 ± 1.8
	c. 29-39	32	.34	0.55 ± 0.26
	d. 40-50	25	.24	0.58 ± 0.46
	e. 56-78	19	.45 ^b	1.6 ± 0.6
	f. 79-134	32	.47 ^c	0.22 ± 0.06
II Diameter at disap- pearance of outer nodes	a. 7-20	35	.08	0.10 ± 0.22
	b. 26-28	67	.07	0.40 ± 0.70
	c. 29-39	80	.34 ^c	0.55 ± 0.16
	d. 40-50	74	.14	0.33 ± 0.28
	e. 56-78	147	.52 ^c	0.96 ± 0.11
	f. 79-134	96	.23 ^b	0.11 ± 0.05

^a N, size of sample; r, correlation coefficient; b, regression coefficient, change of character in millimeters per 1 cm. of strata. ^b Significant. ^c Highly significant.

For the terminal diameter (character I), the table shows that change was certainly occurring while strata groups *e* and *f* were laid down and that the regression was considerably faster in *e* than in *f*. It does not show that any change occurred in *a-d*, inclusive, or whether the regression was then faster or slower than in *e* and *f*. For the diameter at disappearance of outer nodes (character II), change is shown to have occurred in *c*, *e*, and *f*, and regression was faster in *e* than in *f*. In *c* the rate was probably intermediate, but it is not certain that it was either slower than in *e* or faster than in *f*. The rate was probably slower in *a* than in *e*. Both characters I and II were evolving at about the same rate and accelerated and decelerated together.

Since these rates are relative to thicknesses of strata, the demonstrated changes in them may mean either that rate of evolution changed or that rate of sedimentation changed. If the two characters were not correlated with each other, the tendency for rates to vary together would suggest (but not prove) that the variation was mainly in sedimentation. In fact, they are highly correlated with each other ($r = +.66 \pm .15$ for beds 65-70, where the greatest change in regression occurs, and $r = +.85 \pm .02$ for the whole sequence). Other data show that there are, for some characters at least, real changes in rate

of evolution. For instance, in the subgenus *Kosmoceras* (*Anakosmoceras*) regression of the "bundling index" (*Bündelungsziffer*) is negative in strata 1080-1093 and positive thereafter, a change that cannot be caused by rate of sedimentation. In other cases a fairly high positive regression is followed or preceded by one so nearly zero over so long a sequence of strata that explanation by rapidity of sedimentation is incredible. For instance, after strata 26-134 of the table, in which it shows well-marked regression, terminal diameter in *Kosmoceras* (*Zugokosmoceras*) shows no significant regression from 136 to 380, a sequence of strata more than 2½ times as thick.⁴

The ammonites form one of the groups in which great regularity of evolution, as to both direction and rate, have been claimed. Brinkmann's materials afford exceptionally good conditions for the demonstration of this regularity, if it exists, and his data are remarkably complete and objective. Although they cannot rigidly prove irregularity, because alternative explanations cannot be completely ruled out, they strongly suggest it. In any event, they fail to confirm the usual conclusion, based on fewer observations and far more subjective methods of inference.

ORGANISM RATES

Direct determination of rate of evolution for whole organisms, as opposed to selected characters of organisms, would be of the greatest value for the study of evolution. Matthew wrote, nearly a generation ago (1914), "to select a few of the great number of structural differences for measurement would be almost certainly misleading; to average them all would entail many thousands of measurements for each species or genus compared." On the basis suggested in this quotation, the problem would be immediately soluble in theory and probably also in practice, because the taking of thousands of measurements is not an insuperable difficulty and there are now methods for reducing them to coherent and easily manipulated form. As the situation is now understood, the most serious difficulties are (1) selecting unit characters for measurement, (2) reducing them all to metrical form in comparable units, and (3) weighting them in order to obtain a valid

⁴ This character, like several others, also shows reversal of trend; but, since it occurs during a hiatus, this may have been caused by local extinction and reappearing by a less progressive stock from elsewhere.

general average. Many paleontologists and zoologists have proceeded as if everything that can be measured or observed as a unit were a unit character. As preceding examples show, some characters, in this sense, are highly correlated with each other, some slightly correlated, and some independent. In study of the organism as a whole, some account must be taken of these correlations in determining the number and nature of unit characters. Some criterion of classification is needed. For instance, hypsodonty is an important unit character on the criterion of selection value, but morphologically it is the resultant of two other characters which are correlated in one way and uncorrelated in another, and genetically it is undoubtedly controlled by at least two and probably many genes that simultaneously control other, quite distinct phenotypic characters. Characters such as tooth pattern, color, cranial angulation, number of vertebrae, and length of limbs cannot be measured in the same units and must be reduced to a common relative form before averaging is possible. Some essential characters, such as tooth pattern, are difficult to measure in any unit. Finally, an unweighted average might be very misleading because some morphological characters are more crucial, more constant, more independent, more strictly hereditary, and so forth, than others.

It cannot be said that the problem is quite insoluble, but certainly it is so complex and requires so much knowledge not now at hand that no solution is in sight at present. It is still true, as when Matthew wrote, that subjective judgment of the total difference between organisms is (if made by an able and experienced observer) more reliable than any objective measurement yet devised. Obviously, only rough approximations can be made in this way; but an approximation, recognized as such, is more useful than a seemingly exact but really spurious average or no measure at all. Insofar as it seeks to divide phyla into generic and specific stages, representing roughly equivalent amounts of total morphological change, the taxonomic system is a rich source of such data. The assumption that two successive or related genera do cover equivalent amounts of evolution is obviously very uncertain in any one instance. It becomes more reliable and useful when the taxonomists involved are of equal and great skill, when one student with extensive first-hand knowledge has revised all the genera, and especially when a large number of genera based on more or less comparable criteria can be averaged. For such purposes genera are the most useful

units. For paleontological materials, at least, they are more clearly defined and more nearly comparable than any others at present, and they fill the further requirements that they are intended to be essentially monophyletic in origin, to have an extension in time, and to be horizontally divided from preceding and following units of the same rank.

If all genera were strictly comparable, organism rates of evolution would be proportional to the reciprocals of the durations of the genera in question. For a sequence of successive genera, a more reliable value would be obtained by dividing number of genera by total duration. Thus in the line *Hyracotherium-Equus* (but omitting *Equus* because its span is incomplete and indeterminate) there are eight successive genera according to good modern classifications (e.g., Stirton 1940). The time covered is about 45,000,000 years, and the average rate can therefore be expressed as .18 genera per million years, or reciprocally as 5.6 million years per genus.

Strictly comparable averages can only be obtained for genera that arise at known times from known ancestors and that disappear not by extinction, but by evolution into other genera. The number of such genera now known in any one group is small. Some comparisons are nevertheless possible as suggested by the data in Table 3.

TABLE 3

RATES OF EVOLUTION IN HORSES, CHALICOTHERES, AND AMMONITES IN TERMS OF NUMBER OF GENERA PER MILLION YEARS

Group or Line	Number of Genera*	Average Genera (in one line); per Million Years	Phylogeny and Classification Used as Basis
<i>Hyracotherium-Equus</i>	8	.18	Stirton 1940
Chalicotheriidae	5	.17	Colbert 1935
Triassic and earlier ammonites	8	.05	Swinnerton 1923 and others

* With approximately known time of origin and time of transformation into another genus.

With due allowance for all the uncertainties involved, it is safe to conclude that the rate of evolution in chalicotheres was about the same as in horses and that it was faster in both groups of perissodactyls than in the early ammonites.

Analogous estimates of changes in rate within a single line are less useful and require weighting. Matthew (1914) tried this with horse genera, although his purpose was the reverse of the present attempt: he postulated a uniform rate of evolution and attempted to estimate lapses of time by relative amounts of evolution. Matthew's figures were severely criticized by Abel (1929) first because of their subjective and approximate value, and, second, because of some differences of opinion, e.g., that the step *Parahippus-Merychippus* should have been relatively longer, *Eohippus-Orohippus* and *Orohippus-Epihippus* relatively shorter. Despite the very rough nature of such approximations, which was freely admitted by Matthew as it is here, they do have considerable interest and an attempt to revise the estimates on more recent data may have some value.

TABLE 4

ESTIMATES OF CHANGES IN RATES OF EVOLUTION IN GENERA OF HORSES

Genus	A ^a	B	C	D
<i>Equus</i>	10	7	6	1
<i>Pliohippus</i> ^b	10	11	10	1
<i>Merychippus</i>	15	18	6	3
<i>Parahippus</i>	5	5	4	1
<i>Miohippus</i>	5	5	4½	1
<i>Mesohippus</i>	15	16	4½	4
<i>Epihippus</i>	10	9	5	2
<i>Orohippus</i>	10	9	5	2
<i>Hyracotherium</i> ^c				

^a A, Matthew's weighting, on a basis of an average weight of 10 per genus. In each case the weight is understood to be for the approximate total advance to the midpoint of this genus from the midpoint of that preceding. B, similar weights adjusted to subsequent criticism and discovery. C, estimates of approximate time involved, in millions of years. D, rates obtained by dividing the adjusted weights (B) by the approximate time (C).

^b *Hipparion* in Matthew. *Pliohippus* is now known to be nearer the direct line and its evolutionary stage is roughly comparable.

^c *Eohippus* in Matthew. *Eohippus* and *Hyracotherium* are now believed to be synonymous.

On the whole, the rates thus obtained are reasonable relative values, at least to the point showing more rapid average evolution in the middle to late Eocene than subsequently and acceleration in the late Eocene to early Oligocene and early to middle Miocene.

Reverting to Matthew's original purpose, Table 5 gives estimates of the lengths of the Tertiary epochs, except Paleocene, postulating a total of 45,000,000 years.

It seems almost certain that the Miocene was considerably longer

TABLE 5

ESTIMATES OF DURATIONS OF TERTIARY EPOCHS

	In millions of years		
	A ^a	B	C
Pliocene	10	8	9
Miocene	11	13	13
Oligocene	7½	8	7
Eocene	16	16	15

^a A, based on horse genera, Matthew's weighting, on his hypothesis of uniform evolution. B, same, revised weighting (B of preceding title). C, independent estimates based on a balance of all available evidence (sedimentation, radioactivity, general faunal change, etc.).

than the Pliocene and that the estimates based on Matthew's weighting and hypothesis are defective to that extent (but this may be partly due to a different placing of the boundary, on which Matthew frequently changed his usage). The general agreement of all three estimates, except for this one point, is striking. Agreement between the adjusted weights and the independent estimates suggests that the average rates of horse evolution in each epoch did not differ greatly despite acceleration and deceleration during periods that were less than an epoch or that overlapped epochs.

A number of rather isolated approximations of organism rates of evolution have been accumulated from the study of degree of taxonomic differentiation of groups that moved away from a parent stock at approximately known times. An example fairly typical both in its positive and its negative aspects has recently been provided by Doult (1942). A stock of the normally marine seal *Phoca vitulina* became isolated in a fresh-water lake in northern Canada at a time variously estimated at 3,000 to 8,000 years ago. The average length of generations in this species is unknown, but it is probably five to ten years. These lake seals have thus been isolated for from 300 to 1,600 generations, or, as a mean estimate, for approximately 1,000 generations. They are in some respects outside the known range of variation in the survivors of the parent marine stock, and their general morphological differentiation is given subspecific rank. Scattered data on rodents similarly isolated (for instance, on islands) give roughly comparable results and suggest that approximately subspecific morphological differentiation may occur in even less than 300 generations, the lowest figure warranted for these seals.

If such observations can be multiplied and made more precise, they may establish a maximum organism rate for various groups. The conditions that provide such data are, however, unusual historic accidents, and considerable hesitation is proper in considering the bearing of such cases on rates of evolution under more normal circumstances.

Something may also be learned of organism rates from the study of events such as the entrance of North American animals into South America in the Pliocene and the Pleistocene. Many mammals in stocks that entered the southern continent between one and two million years ago have developed endemic genera there, but none has developed endemic families. The conclusion is therefore justified that this length of time has sufficed for generic, but not much higher, differentiation under these circumstances and for these groups, e.g., cricetine rodents, procyonid carnivores, and deer. It is curious that this example gives no clear evidence for the more rapid evolution of animals with shorter generations. For instance, the small rodents apparently did not evolve more rapidly than ungulates with generations several times as long.⁵

Much of the evidence of this sort is so vague and unsatisfactory that its interpretation is almost entirely subjective, and the same facts may be used to reach diametrically opposed conclusions. Thus the great endemism in faunas of isolated Pacific islands has been cited as exemplifying slow evolution on very old islands and also as proof that evolution has there occurred very rapidly (e.g., Zimmerman 1942).

GROUP RATES AND SURVIVORSHIP

Estimates of the average duration of genera within a phylum, as above, are one sort of group rates of evolution and on the whole probably the most satisfactory when obtainable. They are, however, greatly limited by the small number of genera for which both ancestral and descendent genera are surely recognized. Use of all the genera of a larger taxonomic group introduces other sources of error: (1) most genera certainly have a fossil record shorter than their real duration; (2) the numerous genera that disappeared by extinction cannot, on the average, have undergone evolutionary changes comparable to those of genera that disappeared by transformation; and (3) the fossil record of more slowly evolving genera probably is in general more

⁵ The rodents have a greater number of endemic genera, but the genera are no more distinct morphologically.

complete than that of rapidly evolving genera in the same group. The first two sources of error will tend to make estimates of rate too high, and the last to make them too low. The extent of compensation by these opposite tendencies cannot be determined. The errors are, however, systematic and more or less independent of the particular nature of the fossils in question. Thus, they deprive the rate estimates of absolute accuracy, but do not necessarily invalidate the estimates as relative rates in the comparison of different groups. With all their shortcomings, such data do prove to have considerable value and to reveal facts of great importance both for tempo and for mode of evolution, as will be shown.

To explore and illustrate the possibilities, two very different groups

TABLE 6
DISTRIBUTION OF GENERA OF PELECYPODA
Figures are numbers of known genera

		LAST KNOWN APPEARANCE									TOTALS, FIRST KNOWN APPEAR- ANCES	
		<i>Ordovician</i>	<i>Silurian</i>	<i>Devonian</i>	<i>Carboniferous</i>	<i>Permian</i>	<i>Triassic</i>	<i>Jurassic</i>	<i>Cretaceous</i>	<i>Tertiary</i>		<i>Recent</i>
	Ordovician	13	8	6	1	0	4	0	0	0	1	33
FIRST KNOWN APPEARANCE	Silurian	..	17	13	0	1	2	1	0	0	4	38
	Devonian	30	10	4	5	1	0	0	4	54
	Carboniferous	16	3	0	0	1	0	3	23
	Permian	3	1	0	1	0	3	8
	Triassic	30	6	12	0	20	68
	Jurassic	25	12	3	16	56
	Cretaceous	37	0	24	61
	Tertiary	18	64	82
	Totals, last known appearances	13	25	49	27	11	42	33	63	21	139	423

TABLE 7
 DISTRIBUTION OF GENERA OF CARNIVORA (EXCEPT PINNIPEDIA)
 Figures are numbers of genera

		LAST KNOWN APPEARANCE																		Total First Known Appearances
		Paleocene			Eocene			Oligocene			Miocene			Pliocene			Pleistocene	Recent		
		L	M	U	L	M	U	L	M	U	L	M	U	L	M	U				
Paleocene	L	5	0	0	1	6
	M	..	12	0	1	13
	U	5	3	8
Eocene	L	8	5	3	16
	M	7	4	11
	U	13	6	1	0	0	0	2	22

		FIRST KNOWN APPEARANCE																		Total last known appearances
		Oligocene			Miocene			Pliocene			Pleistocene	Recent								
		L	M	U	L	M	U	L	M	U										
Oligocene	L	9	1	4	5	2	0	1	22
	M	3	3
	U	0	3	1	4
Miocene	L	20	0	3	2	25
	M	9	3	7	1	1	1	1	..	22
	U	8	8	1	0	0	0	2	19
Pliocene	L	23	5	4	1	1	7	40
	M	4	2	0	0	2	8
	U	4	2	3	3	9
Pleistocene	L	15	19	..	34
	M
	U
Total last known appearances		5	12	5	13	12	20	15	5	4	28	14	14	41	11	11	19	33	..	262

may be taken: pelecypod molluscs and carnivorous placental mammals (excluding the pinnipeds, for which the record is wholly inadequate). The raw data consist of the geological distributions of all the known genera in each group. These data are summarized in the accompanying tables, in which the numbers of genera running through any given sequence of the geological time scale are entered. Data on pelecypods were gathered chiefly from the latest editions of the standard Zittel, *Grundzüge*, in German, English, and Russian revisions. These genera are broadly drawn and not exhaustively listed, but the data are sufficiently good for present purposes and prove to be adequately enlightening. Data on carnivore genera are more complete and accurate, having been taken from my unpublished classification of mammals, which in turn is based upon almost all the literature of the subject. In both cases the many recent genera that are not known as fossils are omitted. Among the pelecypods, genera unknown before the Pleistocene are also omitted, and the Pleistocene data for the carnivores are less complete than for the Tertiary and not entirely comparable.

Because the lengths of the various periods and epochs differ greatly, these tables do not directly yield estimates of rates of evolution. The geological ages must be translated into terms of relative or absolute time, which introduces another source of error, since this translation cannot as yet be exact. The available estimates of geological chronology are, however, good enough to warrant their use. For estimates of relative durations see, e.g., Schuchert and Dunbar (1933), and for the present status of absolute age measurements by radioactivity see Goodman and Evans (1941).

One interesting method of presentation and analysis of these data after statement in terms of years of duration is by modified survivorship curves (as explained, for instance, in their customary form in Pearl 1940). One method of construction of such curves adapted for the present use is shown by the solid lines in Fig. 5. Here only genera now extinct are counted, and the plotted points represent the percentage of all these genera with a given known duration equal to or higher than the various stated numbers of years. The actual curves approximating these points have been roughly sketched in by eye. Although similar in form, the curves for pelecypods and carnivores differ greatly in extent, the mean survivorship for a genus of Pelecypoda being 78 million years and for a genus of Carnivora only $6\frac{1}{2}$ million years.

The data undoubtedly exaggerate the difference, for various reasons, but it is safe to say that carnivores have evolved, on an average, some ten times as fast as pelecypods.

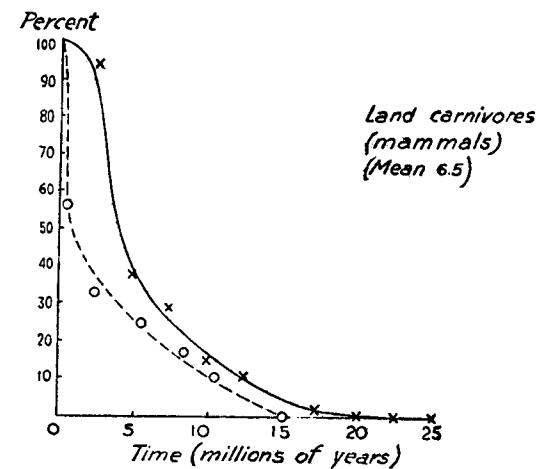
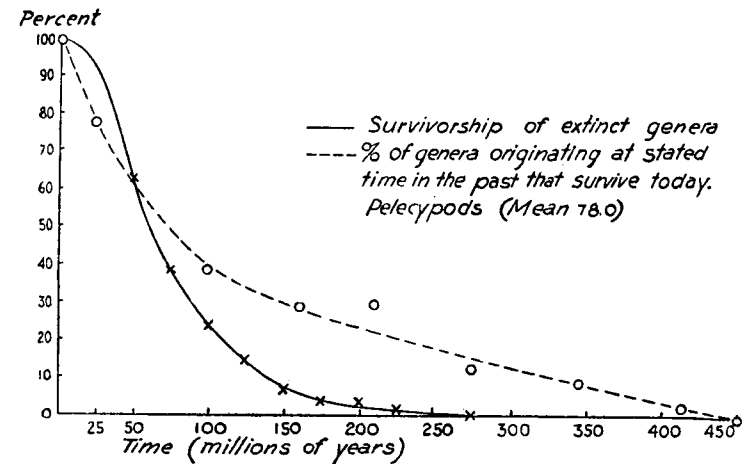


FIG. 5.—Survivorship curves for genera of pelecypods and of land carnivores. Continuous lines, survivorship in genera with completed span (extinct); broken lines, survivorship on basis of ages of genera now living (and known as fossils). Crosses and circles are calculated values to which curves are roughly fitted. Arithmetic co-ordinates; time scale absolute.

The similarity of the curves is more clearly shown and the existing differences are revealed by replacing the absolute time dimension by deviations expressed in percentage of average survivorship, as in Fig. 6

(Pearl 1940). For further comparison an analogous curve for survivorship in a population of mutant *Drosophila* is also given and is found to be closely similar to the generic survivorship curves, especially that for pelecypods. The *Drosophila* curve is based on life spans of individual flies and so is only analogous to the generic curves, not homologous; but the latter might be said to give a picture of a sort of evolutionary metabolism in the two groups concerned, much as the

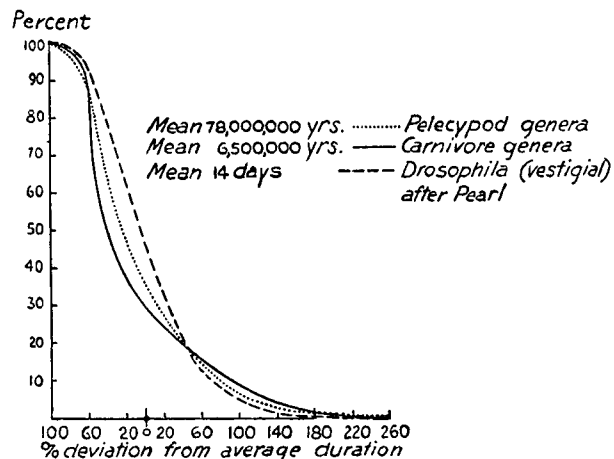


FIG. 6.—Survivorship in pelecypod genera, land carnivore genera, and *Drosophila* individuals. Reduced to comparable form with mean survivorship of three groups coinciding on scale and time represented by percentage of deviation from this point.

Drosophila curve portrays a sort of vital metabolism in the corresponding population.⁶

Analogous curves can be constructed on the basis of living genera that are also known as fossils. In this case the points are plotted as the percentages of such genera that were in existence at the stated times in the past. In other words these points and the sketched curves (broken lines in Fig. 5)⁷ represent the length of time living genera

⁶ This does not involve and is not intended to endorse the interpretive use of the supposed analogy between the individual life cycle and the so-called racial life cycle, an analogy that seems to me misleading and commonly misused. Similarity in shape of the curves has no bearing on similarity of the vital or evolutionary processes producing them, as is amusingly illustrated by Pearl (1940, Fig. 84), who shows that survivorship of automobiles follows almost the same pattern as that of cockroaches. A similar fallacy underlies Willis's evolutionary interpretation of his "hollow curves" (1940).

⁷ The fit is not as smooth as in the other curves, probably because of the smaller number of genera involved.

have now survived. If the recent faunas were random samples of populations similar, as regards generic survivorship, to the extinct genera of the same groups, curves constructed in this way should approximately coincide with those constructed in the previous way. Obviously they do not coincide, and the differences are significant for the study of evolution. These differences are perhaps shown still more clearly in Table 8, in which the expectation of survival is based on the generic survivorship curves for extinct genera.

TABLE 8

EXPECTED AND ACTUAL GENERIC SURVIVORSHIP IN PELECYPODA AND CARNIVORA

Time	Genera Appearing	Percentage of Approximate Expectation of Survival to Recent	Expected Survivals	Actual Survivals
CARNIVORA				
Early Miocene	..	0	0	0
Middle Miocene	22	2	0	0
Late Miocene	19	15	3	2
Early Pliocene	40	23	9	7
Middle Pliocene	8	37	3	2
Late Pliocene	9	90	8	3
Pleistocene	34	98	33	19
PELECYPODA				
Ordovician	33	0	0	1
Silurian	38	0	0	4
Devonian	54	0	0	4
Carboniferous	23	0	0	3
Permian	8	2	0	3
Triassic	68	3	2	20
Jurassic	56	6	3	16
Cretaceous	61	24	15	24
Tertiary	82	88	68	64

Among the carnivores, survival to Recent agrees sufficiently with expectation for genera that appeared before late Pliocene, but it is much lower than expectation for late Pliocene and Pleistocene genera. The discrepancy was largely, perhaps wholly, caused by the unusually high mortality of the Pleistocene. Among recent pelecypods, on the other hand, survival from the Tertiary agrees well enough with expectation, but survival from all previous periods back to the Ordovician inclusive, is greater than expectation. This means that the living pelecypod fauna, far from having experienced increased mortality, as

have the carnivores, includes a large number of very slowly evolving genera and that these slowly evolving lines are less likely to become extinct than are other pelecypods—a striking point of unusual importance, to be discussed in a later section of this study.

Data of this sort also have bearing on differences of rates of evolution within the same group at different times. Although they do not directly measure rates of evolution, it seems probable, a priori, that the number of genera at any one time, the number of genera appearing per million years (rate of origin), and the number disappearing per million years (rate of disappearance) would all be positively correlated with rate of evolution and that the average age of genera at any one time would be negatively correlated with rate of evolution. In Table 9 these figures are given for the Carnivora.

The figures for Lower Paleocene, Pleistocene, and Recent are not exactly comparable with the others.⁸ Disregarding these three times,

TABLE 9
SURVIVAL DATA FOR THE CARNIVORA

Time		a. No. of Genera Existing	b. Rate of Origin	c. Rate of Disap- pearance	d. Average Age of Existing Genera
Paleocene	E ^a	6	1	1	2.5
	M	14	3	2	2.7
	L	10	2	1	3.5
Eocene	E	21	3	3	3.8
	M	19	2	2	3.6
	L	29	4	4	3.6
Oligocene	E	31	8	6	2.2
	M	19	1	2	3.1
	L	18	1	1	4.4
Miocene	E	39	6	6	4.0
	M	33	5	3	4.3
	L	38	5	3	3.5
Pliocene	E	64	13	14	3.8
	M	31	3	4	3.7
	L	29	3	4	4.9
Pleistocene		52	(34)	(19)	(2.7)
Recent ^b		33	3.4

^a E = early; M = middle; L = late.

^b Counting only genera identified in early Pleistocene or earlier.

⁸ Carnivores first appeared in the Lower Paleocene and then necessarily had all four figures unusually low, regardless of rate of evolution. The Pleistocene data are not quite

TABLE 10
STATISTICAL SUMMARY OF REPRESENTATIVE DATA ON CARNIVORE
EVOLUTION^a

	R	M	σ
Number of genera	10-64	28.2 ± 3.5	13.1 ± 2.5
Origination rate	1-13	4.2 ± 0.8	3.1 ± 0.6
Disappearance rate	1-14	3.9 ± 0.8	3.2 ± 0.6
Average age	2.2-4.9	3.65 ± 0.18	0.66 ± 0.12

^a That is, data by stages from Middle Paleocene to Late Pliocene, N = 14 stages in each case.

columns *a*, *b*, and *c* of Table 9 are all highly correlated with each other, as was expected ($r_{ab} = .88$; $r_{ac} = .91$; $r_{bc} = .94$). On the reasonable hypothesis that they are also correlated with the group rate of evolution, the rate of evolution of the carnivores as a whole had three peaks during the Tertiary, in (or just before) early Oligocene, early Miocene, and, especially, early Pliocene; at these times all three of the pertinent figures (columns *a*, *b*, *c* of the Table 9) were simultaneously above their respective means.

Contrary to expectation, column *d* of the table is not significantly correlated with any of the other three columns. Statistically its fluctuations could be purely random. Biologically it is certainly a result of the factors entered in columns *a*, *b*, and *c*; but the relation is too complex and for each item in column *d* extends backward throughout too many different items in the other columns for simple analysis of the relationship.⁹ The average age of existing genera is an indirect, approximate measure of average group rate of evolution over an indefinite period prior to the time of reference, but changes in this measure do not, in this particular instance, reliably indicate changes in rate of evolution within the group. Averaging over longer periods of time may give some information on this point, but here the data on average age do not mean much more than the single figure for mean survivorship previously obtained. Average age should tend to be approximately one-half the mean survivorship for the same statistical population.

complete, and the Pleistocene was much shorter than any previous epoch and otherwise exceptional. The Recent is practically a point in time, and so its data cannot be compared with figures based on duration.

⁹ I have made numerous and lengthy attempts to demonstrate the relationship and also to formulate some comparable and valid measure that would show the expected correlation, but the results were negative and therefore are not included.