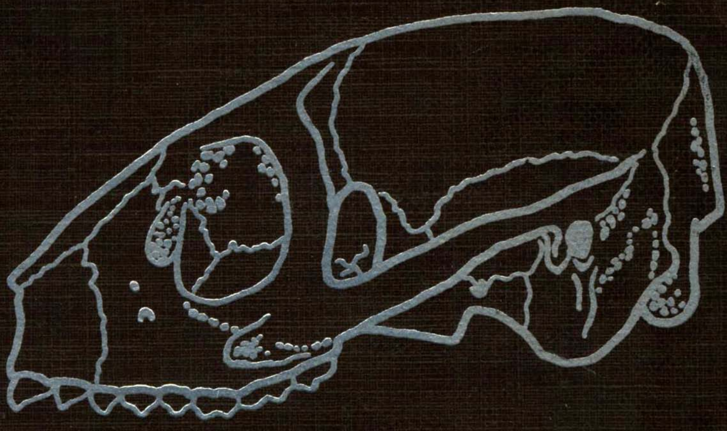

Evolutionary History of the Primates

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PREFACE

We present in this volume a documentation and analysis of the fossil record and evolutionary history of the primates. It is our hope that this effort will in some way balance the generally available literature on primate evolution, which is predominantly concerned with living species.

The training and experience we bring to the making of this book are largely those of paleobiologists, students whose main concern has been the study of fossil samples to determine their taxonomic status, phylogenetic relationships, adaptations, and ways of life—in short, a desire to understand why the bones, teeth, and other features of animals are the way they are.

The vast majority of books on primates were written by students of living species who are either ethologists, anatomists, or anthropologists. As a result, we believe many works tend to be influenced by a view that members of past radiations are "side branches," "bizarre" relict forms related to the "real" living ones, or, even worse, taxa to be judged by their varying degrees of relevance to human evolution. Although understandable as outgrowths of the interest in the evolution of our own species, such anthropocentricity and neontological bias have resulted in studies of the Primates that are neither objective nor justifiable concerning the validity of results obtained. Often, the time, effort, and excellent know-how that go into primate studies are merely channeled into inquiries as to the relevance of the species studied to hominid evolution. Zoologists and paleontologists who study primates can offer a valuable service to anthropology (a science properly concerned with the evolution of humans) by attempting to understand the evolutionary history of individual primate species in their own right. From such studies anthropology may derive lasting benefits for the study of man.

The philosophy underlying the preparation of this work has been the desire to present as much information as possible in one volume on the fossils, on primary systematic hypotheses and their tests by known facts. Anecdotes on personalities, histories of erudite debates and opinions, and many other literary (but nonscientific) sidelights that usually fill volumes on fossil primates and fossil man have been omitted.

This book does not attempt to treat the background subjects necessary for a full appreciation of the text. Therefore, some acquaintance with evolutionary biology, methods of systematics, particularly methods of phylogenetic inference, as well as basic mammalian morphology may be necessary. To partially compensate for this approach we offer a glossary in which certain technical terms that may not be within the everyday usage of all scholars are defined.

We have thus designed this book not as a completely self-sufficient work but as a synthesis of available data somewhat less formal than research papers

EVOLUTIONARY HISTORY OF THE PRIMATES

CONTENTS AND SYNOPTIC CLASSIFICATION*

**Modern genera and higher taxa listed here without a page reference are not treated individually in the text but are considered under their respective families.*

INTRODUCTION

The purpose of this book is to place on record in one volume the fossil evidence for primate evolution, primarily to facilitate the understanding of the genealogy, adaptations, dispersal, and taxonomy of the order. Throughout this book we have tried to express the view that paleontology is essentially a biological discipline, that fossils are objects not only to be collected, named, and described, but to be studied for the information they can convey about the evolution and ways of life of these vanished species. Appreciation of a functional approach to the structure of fossils is fundamental to a synthetic view of evolution, which sees evolutionary change largely as a process of adaptation, a molding of behavior, structure, and mechanical function for various biological roles through the action of natural selection. According to this view, ecological divergence and competition between animal stocks lead to behavioral, mechanical, and structural divergences. To understand evolutionary change, therefore, rather than simply to record it, we must attempt to reconstruct as best we can the ecological and behavioral factors preceding, facilitating, and precipitating structural evolution. This process, in turn, depends very largely upon interpreting the functional significance of the physical adaptations (see especially Bock and von Wahlert, 1965; Bock, 1977) preserved by the fossil record of the groups concerned.

The various activities of paleontological research are closely interdependent, yet time and human limitations make its practice multiphased and time-consuming. The discovery and collection of fossils are preceded by planning, geological reconnaissance, and resolution of problems peculiar to the particular locality. Because modern quarrying methods generally involve patient work for crews of varying sizes at any one locality for several field seasons, a relatively complete description of any taxon must await the collection of an adequate sample. The study of the fossils usually focuses on several closely related objectives. The faunistic and biostratigraphic appraisals of all species at a locality or in a faunal level are amalgams of separate studies on the sundry species from many perspectives. In studies on fossils of any one group, probably the most important and certainly the most fundamental problem is the correct delineation of the species.

This alpha taxonomy, the cornerstone of all phylogenetic and adaptational considerations as well as of supraspecific taxonomy, must solve not only problems of geographical and temporal variation in related samples from localities of known stratigraphic relationships, but also problems of variation in the study sample itself. Following alpha taxonomy of fossil species, the ultimate goal of paleobiological studies clearly must concern itself with the explanation of the known attributes of species, employing phylogenetic and adaptational analyses.

It is becoming apparent, even to the most pure taxonomist and to the most conservative descriptive paleontologists, that at least a rudimentary understanding of the functional anatomy of a species has profound effects on the phylogenetic evaluations of its morphology. Mammal teeth have long been yielding phylogenetic dividends when questions are asked about the form and mechanical function of their isolated components, of the whole tooth, or of whole dentitions. A constant evaluation of heritage components, as well as of functional aspects in any biological feature, is necessary when concentrating on the taxonomy, phyletic affinities, or mechanical and behavioral functions of one or more species. While many taxonomic studies suffer from an almost complete neglect of function, equally marred undertakings that concentrate "purely" on functional attributes of biological features also often appear. Unless the geometry of phylogeny is understood in a time-sequential framework, functional studies by themselves are unlikely to yield answers to evolutionary questions. Without a careful and continuous search for and scrutiny of the living and fossil record and the phylogeny of the group, it is difficult to discern the precarious but most important distinction between "heritage" and "habitus" features of living or extinct species.

We may briefly point to the relationship between primarily paleontological studies and more specialized undertakings on fossil specimens. The most advanced available techniques and tools that yield reasonable dividends for time and effort invested should be utilized to study all feasible biological attributes of living and extinct species to elicit functional answers. Only then will it be possible to evaluate fossil taxa to the fullest extent both phylogenetically and adaptationally in the context of their respective faunas. However, these detailed evolutionary or functional analyses of individual remains are based eventually (not only) on the presumably correct allocation of fossils to a particular taxon by the practicing paleontologist. Before cranial, dental, or postcranial elements can be allocated to the Primates, or to a particular subgroup, a great deal of primarily paleontological expertise is employed, with most variables difficult to quantify. Moreover, such studies are often based on phylogenies determined by prior investigations.

There are today a number of conflicting or only partially compatible methods of constructing hypotheses of evolutionary relationships for primates or any other group of organisms (Simpson, 1975); we ourselves are not always in full agreement (Szalay, 1977b; Delson, 1977b). A grasp of both the methodology of and the reasons for the construction of phylogenies and hypotheses of divergence is thus of prime importance for understanding any problem relating to primate biology, especially the ideas we present here. The bases of phylogenetic hypotheses are character analyses, and we may note that in this area of systematics the following levels of observation and decision, and identifiable areas of disagreement, exist (Szalay, 1977b): (1) the existence of a homology; (2) the polarity of a number of homologous states; (3) the weighting of similarities which suggest contrasting hypotheses of relationships (i.e., sorting out relative recency of shared and derived characters).

With these areas of potential disagreement in mind, the following is an attempted summary of the operations involved in character analysis and in choosing one of several competing phylogenetic schemes (Szalay, 1977b):

1. Observations are made (as an indirect result of a host of unexpressed assumptions and hypotheses), and a particular set of circumstances (a character state) is stated to be present in two or more taxa. In other words, characters are recognized and delineated. We can refer to this as data gathering.

2. If these similarities, as originally perceived, can also be recognized by others (i.e.. if they are repeatable), then it may be said that we have an empirical data base.

3. The hypothesis may now be advanced that either the similarity is the result of homology, and, more specifically, that it is the sharing of an ancient (primitive, ancestral) or less ancient (advanced, derived) character, or, if not a homology, that it is convergence. One of these hypotheses is arrived at when alternative character states are compared by an examination of both ontogenetic and adult states, as well as by mechanical analysis of the character. This pivotal phase of analysis requires the use of the biologically most sophisticated methods, techniques, and interpretive schemes. Decisions on this level profoundly affect what is commonly called "testing" of phylogenetic hypotheses.

The determination of polarity along a morphocline and, especially, the role that geochronologic age of relevant fossil taxa plays in this process are among the more hotly debated questions in modern systematics, and our own published views here differ. For obvious reasons (see Simpson, 1975), character states of a given feature are less variable at the onset of its evolutionary transformation, the ancestral condition being dominant. As time passes and adaptation proceeds, character states become progressively more variable and diversified. But can a given state be considered ancestral a priori, on the basis of its relatively great age within a group, or should age be ignored in favor of distribution patterns and outgroup comparisons? In the former view, a working hypothesis (to be rigorously screened by morphological criteria) is based on biostratigraphic evidence in order to serve as an important starting point for the establishment of polarity. On the other hand, it has been argued that, if age is held aside at this point in the analysis, there is less chance of circularity of reasoning; polarity is determined, if possible, without recourse to temporal data, which may be brought into use only when it is not otherwise possible to choose between two potential ancestral conditions. In most cases, of course, the two methods are equivalent, as morphoclines often coincide with chronoclines, but it will be seen from the text that we approach the problems involved in slightly different ways.

4. "Testing" of polarities should proceed beyond character analysis when possible, by comparing the hypothesized polarities of character clines to one another, a method referred to by Hennig (1966) as "reciprocal illumination."

5. With the known or suspected polarities of as many character clines as possible, using shared derived characters, and by weighting the phylogenetic importance of biologically different kinds of shared derived characters, a phylogenetic hypothesis is constructed (using both "sister group" and "ancestor–descendant" concepts, depending on the nature of the evidence). Into this hypothesis one attempts to place the investigated homologies in a relative time framework. When possible, attempts should be made to arrange a phylogenetic hypothesis in a time framework, using all of the available lithostratigraphic and biostratigraphic evidence. It is desirable that this phylogenetic hypothesis should postulate the least number of possible derivations for unique and functionally highly integrated features. That theory of relationships which accounts most parsimoniously for all of the postulated polarities of the known and weighted characters is to be preferred. Should this call for parsimony not be heeded, then nothing prevents one from postulating *any* phylogenetic hypothesis, whatsoever.

When one considers all of these factors in hypothesis formulation, then one conforms most closely to the notion (Popper, 1965) of striving for hypotheses with high information content and easy testability. Contrary to some statements on the alleged untestability of ancestor–descendant hypotheses and the alleged irrelevance of functional studies, consideration of the temporal data inherent in the fossil record, along with the assessment of the biological roles of characters whose distribution is analyzed, may assure the greatest possible information content for phyletic hypotheses. Once again, our approaches to the discerning of actual ancestor–descendant relationships among known species differ somewhat, involving varying emphases on either a probabilistic analysis of multiple criteria or a parsimony-based view which also takes into account stratigraphic successions (compare Delson, 1977b, and Szalay, 1977a). Whatever the specifics, the inclusion of all possible data in a phyletic hypothesis or a scenario will certainly result in the most desirable statement about the relationships and adaptations of the taxa involved.

Classifications must obviously reflect the underlying phylogeny, but the details of this reflection again are the subject of much debate. We basically agree that related taxa should be classified together, and that taxa should be monophyletic or, when possible, holophyletic (see Glossary) and definable by a set of derived characters in common. But we both also recognize the value of patristic affinities and distinctions based on divergence. In general, such deviations from a "purely" genealogical classificatory practice will be clear from the attendant discussions.

It is our intention to employ the preceding methodology throughout the main text of this book, a systematically organized account of each primate taxon known in the fossil record. This introduction has so far laid the philosophical groundwork underlying our approach, and the following section will present the chronological framework within which all fossils can be placed.

The systematic treatment follows a standardized pattern which can be outlined here. The basic unit of discussion is the genus, long recognized as having more practical significance in paleontology than do species. For each genus and higher taxon, a complete synonymy is given, followed by the time and space distribution of each taxon and the major subtaxa included therein. The discussion then includes the diagnostic features of the group or genus, its distinctions from close relatives, phyletic position within the next higher taxon, underlying adaptations and evolutionary pattern, and major morphological distinctions within the taxon itself.

The synonymy lists each different taxonomic name (*nomen*) by which previous authors referred to the taxon involved or a major component thereof. A name in the format "*nomen* author, date" implies that the stated author coined the name and used it to refer to one or more specimens or taxa now included in the taxon under consideration, which may be termed the senior synonym. On the other hand, an entry in the format "*nomen* author, date: author, date" implies that the nomen was coined by the first author but that the second author employed that name to refer to all or part of the taxon under discussion. In some instances, the name of the first author is left out, especially if it is cited elsewhere in the same section (genus or higher taxon); the format is then "*nomen*: author, date." The term "in part" following an author implies that his concept included all or part of the taxon under consideration, as well as other taxa. The term "*nec*" in the format "*nomen* author, date, *nec* author, date" means that the first author coined a supposedly new name which in fact had previously been coined by the second author; the former name, which referred to all or part of the taxon under consideration, is a junior homonym and has no taxonomic value. A *nomen nudum* is a name that has no status in taxonomy, because it does not satisfy the criteria for availability of the International Code of Zoological Nomenclature (Stoll *et al.*, 1961), the rulebook of animal systematics. Such names, if for a genus or species, are not italicized here but may be placed in quotation marks to set them apart from available names. Quotation marks may also be used to indicate that a genus or species is not really the same as the taxon whose name is being used, but that the different form has not been formally named; an example is the Miocene cercopithecid "*Victoriapithecus*" *leakeyi*, which is probably not a species of the same genus as *Victoriapithecus macinnesi*, but *leakeyi* was originally named in the genus *Victoriapithecus* and has not yet been given a distinct generic name. Uncertainty of reference at the genus or species level may be indicated by the use of such symbols as "?," "cf.," or "aff." The meaning of these symbols varies among authors, but, in general, a "?" placed directly in front (or behind) a generic name implies uncertainty as to whether the species involved belongs to that genus, while a queried species implies uncertain reference of specific specimens to that species. The Latin abbreviations cf. (for "*confer*," or compare) and aff. (for "*affinis*," or related) usually indicate greater or less doubts as to the correct placement of a sample of specimens in a given species. Each different name is set off in our synonymies by a period (.). A semicolon (;) is used to set off multiple usages of the same nomen and/or misspellings or lapses (lapsus). Not all usages of the same nomen are included, only those (for some genera) which referred to newly described fossil material. In the synonymies and in our choice of senior synonyms, we have been guided by the rules and recommendations of the Code; further discussion of these points may be found in a text such as Mayr (1969).

Following the synonymy is given the distribution of the taxon under discussion. The time range is listed first, by epoch or subepoch, followed by a mammal-age term when possible. Geographic range is presented by continent and region or country. For higher taxa, the next line lists included taxa of the next lowest rank employed in our classification (e.g., tribes in a subfamily or genera in a tribe). For genera, this line is only employed if subgenera are recognized, in which case the synonymy of the genus as a whole may be left out. The species known for that genus are then listed, in order of taxonomic priority after the type species; if there is more than one in the genus, they are numbered. For each species, a list of fossil localities is presented, in stratigraphic order from oldest to youngest. Each locality name is followed by a number in parentheses, which corresponds to its position in the locality list given later in this introduction. The type locality is indicated by a star (⋆) following its name. If the specimens from a given locality are only questionably referred to the species, then the name may be preceded by "?," (cf), or (aff.), corresponding to the synonymy entry.

The discussion sections for the genera and higher taxa obviously form the bulk of this work, representing our synthesis of all available information on the morphology, relationships, and adaptations of pri-