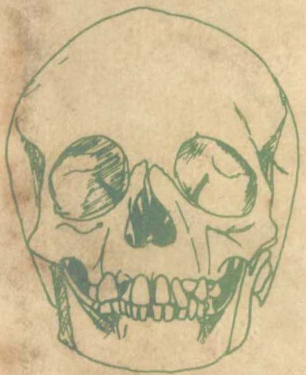
EVOLUTIONARY CHANGES TO THE PRIMATE SKULL AND DENTITION



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Not only does this book provide a unique, comprehensive review of evolutionary changes to the primate skull and dentition, it also carefully analyzes comparative primate dental histology. Throughout this examination, the authors treat the skull as a complex but integral biological entity rather than as a series of discrete morphological entities. The explicit results and far-reaching implications of this approach provide dramatic insight into skull evolution and biological function. It also provides fascinating reading for serious students and practitioners of dentistry, medicine, anthropology, orthodontics, otorhinolaryngology and anatomy.

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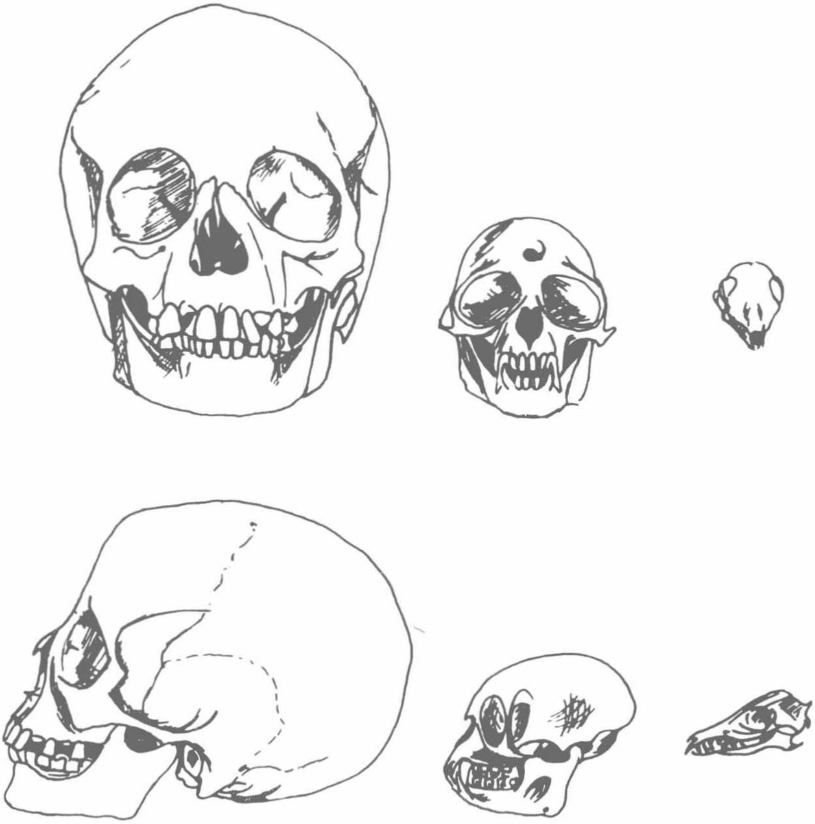

to all those who have interests in the skull, jaws, and teeth: they have a great responsibility in the elucidation of primate evolutionary changes

INTRODUCTION

RECENT YEARS have witnessed a significant improvement in the condition of primate, especially hominoid, nomenclature. This improvement reflects three factors. First, every new fossil has ceased to be regarded by palaeontologists as a new species. Secondly, palaeontologists, zoologists and physical anthropologists have expanded the concept of variability in palaeospecies. Hence, greater ranges of morphological variation are lumped together within a single species. Finally, the International Code of Zoological Nomenclature has been adopted by the majority of workers.

Physical anthropology occupies a pre-eminent niche in biological research. This is not only a consequence of its intrinsic intellectual interest. Indeed, only by critical investigation of extant and fossil primates is it possible to deduce functional and evolutionary data of particular morphological structures (or features). Despite the wealth of literature published each year, however, many fundamental questions have yet to be evaluated. A considerable proportion of the current anthropological literature remains repetitive and contributes little to the understanding of the fundamental principles encompassing primate morphology.

In spite of active and often preferential researches, palaeontological knowledge of primates remains fragmentary. Since primates are fundamentally linked to tropical forests—an unfavorable environment for fossilization—many gaps may never be filled. Nevertheless, the most ancient radiations, and therefore the first radiations, are already better known. We are, therefore, leaving behind the confusion that has enveloped the history of the Hominoidea. Among extant primates, zoologists and biochemists generally agree to recognizing four natural groups, often considered as infraorders: *Lemuriformes*, *Lorisifomes*, *Tarsiiformes*, and *Simiiformes* (Anthropoidea). All post-Eocene fossils, and most of those from the Eocene, can be assigned to one or other of these taxa. It seems, therefore, that the four extant groups differentiated during the early Tertiary. The possible exception is the *Lorisiformes*, which are known since the Miocene only. The more ancient fossils, especially those from the Paleocene, to which must be added their direct descendants in the Eocene, present, together with evidently primitive features, some unexpected specializations in such ancient forms; they represent an early radiation and do not belong to the recent infraorders.

Hominoids—chimpanzee, gorilla, and man—have apparently all evolved during the past five to fifteen million years from a common ancestor, *Dryopithecus*. The field of human evolution is particularly concerned with the particular ecological features which have selected for behavioral and structural traits found in the divergent hominoid line which evolved into *Homo*. Competition in a common environment among sympatric populations of the ancestral species of the Pongidae and Hominidae, along with competition from other primates and carnivores, may possibly have induced a divergence which led to varied econiches for hominids and apes. The geographical econiches distribution of contemporary primates seems to indicate that competitive exclusion has been operating extensively. Gorillas, for instance, live in mountainous regions and are largely vegetarian. Chimpanzees are suited to a terrestrial environment, although they have retreated into forest environments in every region where they have been sympatric with modern man. Baboons are also terrestrial, plain-living animals and, like humans, are carnivorous hunters. Moreover, humans and baboons may have seriously competed for similar food sources at times in their phylogenetic histories. A slightly unequal reliance on different food sources and incipient tool use may, however, have enabled hominid ancestors a competitive advantage while other terrestrial apes came to rely more on woodland-forest environments. Conversely, the pongid ancestors might have competed more successfully in the forest-woodlands and edged the protohominids onto the plains. Once the populations begin exploiting different econiches, however, the resulting allopatry would promote further divergence by limiting gene flow.

Whether dietary specialization or incipient tool use came first is debatable, as is the primary reason for the initial hominid divergence. There is little doubt that once econiche diversity for Miocene apes was effected, the different econiches provided varying opportunities and selective pressures for culture and that culture was instrumental at some point in influencing the divergence of protohominids and other hominids. How this is reflected in the morphology of the primate skull is the subject of this book.

Morphological investigation of extant primates remains the kernel of investigations into fossil specimens. Such investigations are generally limited to techniques of dissection of soft tissues and observations of the hard underlying structures coupled with the association of these to functional behavioral developments. The principal method of studying form still relies on the experienced eye and the creative mind behind the eye. Additional information is often acquired by univariate or bivariate analysis of simple measurements. Combinations of such measurements, in the guise of indices, are frequently computed for the analysis of shape. Such elementary metrical study rarely achieves more than a mere confirmation of data already obtained from subjective visual analysis. Indeed, for accurate objective assessment of skeletal form, many dimensions must be measured coupled with their subsequent analysis by multivariate statistical techniques. Only in this way can differing modes of variation and multivariation coupled with varying kinds of correlation that characterize the metrical definition of complex shape be accommodated.

Multivariate statistical analysis is capable of allowing for such perturbations of data that are difficult to evaluate visually and impossible to reveal visually or by simple measurement alone. There are, however, some restrictions or limitations to the wholesale application of multivariate statistical analysis in morphological studies.

First, measurements only provide data in relation to datum points. They do not provide information about shape between the datum points. Obviously, therefore, an increase in the number of datum points will improve the metrical definition of shape, although there may be practical problems in recording a large number of dimensions.

Second, measurements frequently depend upon the particular orientation of specimens along standard lines or planes. In actual fact, there is no a priori reason why homologous lines or planes may not be curved, with their curves varying in different species. This facet is difficult to accomodate unless both sophisticated measurement and statistical analytical techniques are employed.

Finally, the choice of datum points is always a subject which arouses controversy, since quite frequently the selection is based on subjective intuition. It is obvious, however, that no matter how sophisicated the method of statistical analysis, definitive conclusions depend ultimately on the existence of sound data.

When all the characters are measured, measures of statistical distances between populations are little more than measures of size differences. Distance is, of course, not purely a measure of size difference, since shape and morphology are defined by differential size. But differences of magnitude greatly outweigh the effect of differences of proportion in distances whenever the taxonomic units vary more than a slight amount in size.

Besides the taxonomic shortcomings of pure size differences, they may be further rendered inaccurate or statistically invalid by failure of the raw data to conform to the assumption of distribution normality, large sample size, equality of variance, and linearity and homogeneity of covariance upon which the probability theory depends. The conformity of input data to these conditions is not commonly documented or defended by researchers before the use of statistical routines such as an analysis of variance, factor analysis, and canonical variate analysis. Far more analysis and checking of the original data is therefore required before elegant and sophisticated statistical techniques can be applied.

In addition, there is also the concept of biological variation and the difficulty of obtaining representative samples. Indeed, when dealing with isolated fossil specimens, there is no chance of ascertaining whether the specimen is typical of a population or is representative of an extreme of the population range. Nevertheless, unless a metrical approach is adopted, there is no way that evolutionary studies can be elevated from the subjective to the objective plane.

The purpose of this book is to concentrate on the skull, since compared with the remainder of the skeleton, the cranium, especially the teeth, is preferentially preserved. Also, while considering the skull of primates as a whole, attempts are made to concentrate on hominoids. This results from the fact that hominoid skulls comprise a number of morphological features which have remained controversial for far too long, and it is high time that a more constructive approach was adopted in order to eradicate the majority of these subjective and controversial assessments. Nevertheless, until more hominoid skulls are described and the hominoid evolutionary lineage fully interpreted, an objective interpretation of the important morphological features will remain incomplete. Furthermore, until nonhuman primate skulls received the detailed investigation afforded to human skulls (e.g. Downs, 1956; Bjork, 1960), little objective data will ensue. This book is divided into a number of sections relating to the neurocranium, the facial skeleton, the jaws, and the teeth. Attempts are made, however, to emphasize that the skull is a complex biological unit as a whole rather than a series of discrete biological structures. Far too often, evolutionary changes in one morphological attribute are interpreted without due regard to the biological significance to the skull as a whole.

Relative brain size is defined as the ratio of the actual to the expected brain size. The expected brain size may be computed from the regression equation in which brain size is predicted from body size. Jerison (1970) has analyzed the history of brain size in Teritiary animals and their living descendents. He has shown a continuing increase in relative brain size with carnivores having relatively larger brains than their ungulate contemporaries. This brain size increase has also been shown to parallel the evolution of greater diversity. But despite the evident general trend towards an increase in average brain size, there is an interesting and important overlap in the region of low brain size. This indicates the presence of at least some small-brained species at all times. Thus, the evolution of enlarged brains, though generally a route to success and survival of new species, was apparently not universal even among progressive orders. The key factor is probably that the brain of mammals has evolved in ways appropriate to behavior within particular niches. As more diversified niches were invaded, more diversified brain adaptations evolved. Nevertheless, the fact that some animals continued with a small brain size suggests that the latter does not lead to extinction in some groups.

It is also interesting that, from examination of asymmetry in mountain gorilla skulls (*Gorilla gorilla beringei*), Groves and Walker (1973) concluded that cerebral form and function have little effect on skull shape.

A constant supply of hominoid fossil specimens is being described by Leakey and his coworkers (e.g. Leakey and Wood, 1974), and these may well shed some important light on the pattern of human evolution. There are, however, one or two problems. First, there is an overwhelming need for some growth data on fossil specimens. Even when considering modern man, there is little accurate longitudinal data (Knott, 1972). The second problem is the degree of association between one part of the skull and another. For instance, during growth, associations have been described between the upper and lower jaws (Slavsgold, 1971), the mandible and cranial base (Hoyte, 1971; Droel and Isaacson, 1972; Knott, 1973), and between the nasal septum and jaws (Sarnat, 19700). Thus, there are varying degrees of associations between one part of the skull and another (Solow, 1966; Brown, 1969; Mitani, 1973), although whether there are similar patterns of association in nonhuman primate skulls has yet to be elucidated. In addition to metrical traits, Hertzog (1968) has listed some associations between discontinuous cranial traits.

Although there is considerable data relating to the evolution of human skull form (Bunak, 1968) and many detailed metrical analyses of the human skull (Stoessiger and Morant, 1932; Little, 1943; Tattersall, 1968), the relationship between genetic and environmental factors to skull form has received little study (McKeown, 1974). Nevertheless, from the existence of secular changes in skull form (Barnard, 1935; Ingervall, Lewin and

Hedegard, 1972), it is evident that environmental factors do play a role.

Possibly the most fruitful method of analyzing the degree of variation in skull dimensions involves factor analysis. For instance, from fifty-four measurements of one hundred Anglo-Saxon skulls, Howells (1957) selected three measurements of length, breadth, and height which accounted for 51 percent of the variation in all measurements with the matrix of residual correlations yielding a further seven factors representing regions of variation not related to the influence of the first three. These seven additional dimensions accounted for a further 31 percent of the total variance and included variation in supraorbital development, in forebrain width, in forehead fullness, in fullness across the top of the parietals, in lower occipital fullness and in basal breadth. These ten measurements, therefore, accounted for virtually all of the correlation in the cranial vault proper and each were virtually independent of one another.

In a later study of Egyptian crania, Landauer (1962) extracted five factors from the facial skeleton, one of general size of the skull as a whole, one of the size of skeletal mass and muscular strength, one of the breadth across the malar bones, one of frontal fullness, and one of facial breadth. In another study based on cranial angles and indices, Chopra (1969) compared twenty different cranial series using factor analysis. On the average, five factors covered the total variation, although the factor structure differed considerably from group to group, so that seventeen different factors were identified. These included cranial and facial width, facial relief, cranial ruggedness and the degree of prognathism.

If only a similar study were performed on nonhuman primate skulls, then there might be a considerable advance in the knowledge of primate evolutionary trends.

Dental arches (or dental arcades) have occupied limited status in the study of primate evolution. Possibly one feature responsible for this lack of status stems from the dearth of longitudinal data on the growth changes in the dental arch (Knott, 1972). Nevertheless, an example of the value of the dental arch in primate taxonomy can be illustrated from *Ramapithecus*. Species of *Ramapithecus* are among the few hominoid species currently considered as possibly close to the direct line of human ancestry, with one of the most striking resemblances between *Ramapithecus* and later hominoids being the supposed presence of parabolic dental arches. In a recent study, Walker and Andrews (1973) have reconstructed the dental arcades of *Ramapithecus wickeri*. These indicated very small incisors and posteriorly diverging and nearly straight cheek tooth rows rather widely separated and curved tooth rows such as are found in modern man. The palate is narrow and the tooth rows are relatively very elongated. The premaxillary regions are most abbreviated and a small snout with a small piriform aperture projected from a broad and very flat face which was especially wide in the zygomatic region. These peculiar and unique gnathic features clearly place *Ramapithecus wickeri* apart from contemporary species of *Dryopithecus*.

There is, however, still far too little quantitative data relating to the nonhuman primate dental arch, in particular how dental arch form is related to that of the skull.

Recently there has been a search for factors to discriminate the hard palates between human and nonhuman primates. The size of the foramen incisivum is just one supposedly discriminating feature. From a study of Eskimo and Bavarian skulls, however, Helmuth (1973) has shown that this foramen is partly associated with the size of the palate. This, therefore, emphasizes another feature, namely that size factors must be eliminated as far as possible in order to obtain critical primate taxonomic classifications.

The role of genetic and environmental factors in tooth development has long been controversial (Chung, Niswander and Runch, 1971; Potter, 1972; Anderson and Thompson, 1973; Wickramaratne, 1974; Johanson, 1974; Portin and Alvesalo, 1974). Yet definitive evidence on their respective roles is essential in order to account for the reduction in tooth size during hominid evolution (Sofaer, 1974). Even with the sequence of tooth eruption, there is little data concerning the role of genetic and environmental factors (Garn, Wertheimer, Sandusky and McCann, 1972;

Shumaker, 1974). Nevertheless, in view of the existence of secular changes in tooth size (Eberling, Ingervall and Hedegard, 1973), environmental factors exert some role in dental development, but is it possible that dental and skull development share similar genetic influences?

Tooth attrition has been examined from an experimental (Brace and Molnar, 1967) and cultural (Molnar, 1972) viewpoints. Nevertheless, as tooth attrition is a universal primate phenomenon, it is difficult to ascertain its taxonomic significance. Looking at attrition from another aspect, one of the distinguishing features between robust and gracile australopithecines is traditionally the different chipping of the teeth. From examination of worn deciduous and permanent teeth, Wallace (1973) concluded that there was no significant difference between the chipping of these two forms. This worker therefore concluded that there was no difference in the diet of robust and gracile australopithecines. However, the temporomandibular articulations, the insertions of the muscles of mastication, and tooth size have probably more significance in identifying diets compared with tooth chipping.

From these unanswered questions, it is obvious that despite its illustrious study, there is still little definitive evidence on the evolutionary changes of the primate skull. At the end of this book, therefore, it is hoped that the reader will be convinced of a new direction for his research, particularly in view of the recent fossil finds emanating from Africa (Oxnard, 1975).

REFERENCES

Anderson, D. L. and Thompson, G. W.: Interrelationships and sex differences of dental and skeletal measurements. *J Dent Res,* 52:431, 1973.

Barnard, M. M.: The secular variations of skull characters in four series of Egyptian skulls. *Ann Eugen,* 6:352, 1935.

Bjork, A.: The relationship of the jaws to the cranium. In Lundstrom, A. (Ed.): *Introduction to Orthodontics.* London, McGraw, 1960, pp. 104-140.

Brace, C. L. and Molnar, S.: Experimental studies in human tooth wear. *Am J Phys Anthropol,* 27:213, 1967.

Brown, T.: Facial growth pattern and coordination. *Aust Orthod J,* 2:5, 1969.

Bunak, V. V.: On the evolution of the shape of the human skull. *Vopr Antrop,* 30:3, 1968.

Chopra, V. P.: Faktoren des Craniums bei prahistorischen Populationen. *Homo, 20*:185, 1969.

Chung, C. S., Niswander, J. D., and Runck, D. W.: Genetic and epidemiologic studies of oral characteristics in Hawaii's school children: dental anomalies. *Am J Phys Anthropol, 36*:427, 1971.

Downs, W. B.: Analysis of the dentofacial profile. *Angle Orthod, 26*:191, 1956.

Droel, R., and Isaacson, R. J.: Some relationships between the glenoid fossa position and various skeletal discrepancies. *Am J Orthod, 61*:64, 1972.

Ebeling, C. F., Ingervall, B., and Hedegard, B.: Secular changes in tooth size in Swedish men. *Acta Odont Scand, 31*:141, 1973.

Garn, S. M., Wertheimer, F., Sandusky, S. T., and McCann, M. B.: Advanced tooth emergence in negro individuals. *J Dent Res, 51*:1506, 1972.

Groves, C. P. and Walker, N. K.: Asymmetry in gorilla skulls: evidence of lateralysed brain function. *Nature, 244*:53, 1973.

Helmuth, H.: On the foramen incisivum in *Homo sapiens*: Morphology and phylogenetic aspects. *Homo, 24*:117, 1973.

Hertzog, K. P.: Associations between discontinuous cranial traits. *Am J Phys Anthropol, 29*:397, 1968.

Howells, W. W.: The cranial vault: factors of size and shape. *Am J Phys Anthropol, 15*:19, 1957.

Hoyte, D. A.: Mechanisms of growth in the cranial vault and base. *J Dent Res, 50*:1447, 1971.

Ingervall, B., Lewin, T., and Hedegard, B.: Secular changes in the morphology of the skull in swedish men. *Acta Odont Scand, 30*:539, 1972.

Jerison, H. J.: Brain evolution: new light on old principles. *Science, 170*:1224, 1970.

Johanson, D. C.: Some metric aspects of the permanent and deciduous dentition of the pygmy chimpanzee (*Pan paniscus*). Am J Phys *Anthropol, 41*:39, 1974.

Knott, V. B.: Longitudinal study of dental arch widths at four stages of dentition. *Angle Orthod, 42*:387, 1972.

Knott, V. B.: Growth of the mandible relative to a cranial base line. *Angle Orthod, 43*:305, 1973.

Kurisu, K., Kato, S., and Kanda, S.: A factor analysis of the environmental correlation matrix from the craniofacial traits of male monozygotic twins in growing age. *Med J. Osaka Univ, 22*:207, 1972.

Landauer, C. A.: A factor analysis of the facial skeleton. *Hum Biol, 34*:239, 1962.

Leakey, R. E. F. and Wood, B. A.: New evidence of the genus *Homo* from East Rudolf. *Am J Phys Anthropol, 41*:237, 1974.

Little, K. L.: A study of a series of human skulls from Castle Hill, Scarborough. *Biometrika, 33*:25, 1943.

McKeown, M.: Genetic and environmental influence on the shape of the adult dog skull. *Angle Orthod, 44*:62, 1974.

Mitani, H.: Contribution of the posterior cranial base and mandibular condyles to facial depth and height during puberty. *Angle Orthod, 43*:337, 1973.

Molnar, S.: Tooth wear and culture: A survey of tooth functions among some prehistoric populations. *Curr Anthropol, 13*:511, 1972.

Oxnard, C. E.: The place of the australopithecines in human evolution. *Nature* (Lond), 258:389, 1975.

Portin, P. and Alvesalo, L.: The inheritance of shovel shape in maxillary central incisors. *Am J Phys Anthropol, 41*:59, 1974.

Potter, R. H.: Univariate versus multivariate differences in tooth size according to sex. *J Dent Res, 51*:716, 1972.

Sarnat, B. G.: The face and jaws after surgical experimentation with the septovomeral region in growing and adult rabbits. *Acta Otolaryngol, 268*:1, 1970.

Shumaker, D. B.: A comparison of chronologic age and physiologic age as predictors of tooth eruption. *Am J. Orthod, 66*:50, 1974.

Slavgsvold, O.: Associations in width dimensions of the upper and lower jaws. *Trans Eur Orthod Soc, 71*:465, 1971.

Sofaer, J.: Differential evolutionary reduction of tooth size as a consequence of skeletal reduction. *J Dent Res, 53*:752, 1974.

Solow, B.: The pattern of craniofacial associations. *Acta Odont Scand, 24*: suppl. 46, 1966.

Stoessiger, B. and Morant, G. M.: A study of the crania in the vaulted ambulatory of St. Leonard's Church, Hythe. *Biometrika, 24*:135, 1932.

Tattersall, I.: Multivariate analysis of some medieval British cranial series. *Man, 3*:284, 1968.

Walker, A. and Andrews, P.: Reconstruction of the dental arcade of *Ramapithecus wickeri*. *Nature, 244*:313, 1973.

Wallace, J. A.: Tooth chipping in the australopithecines. *Nature, 244*:117, 1973.

Wickramaratne, G. A.: The 'skeletal profile' and dentition of some inbred strains of mice. *J Anat, 117*:565, 1974.