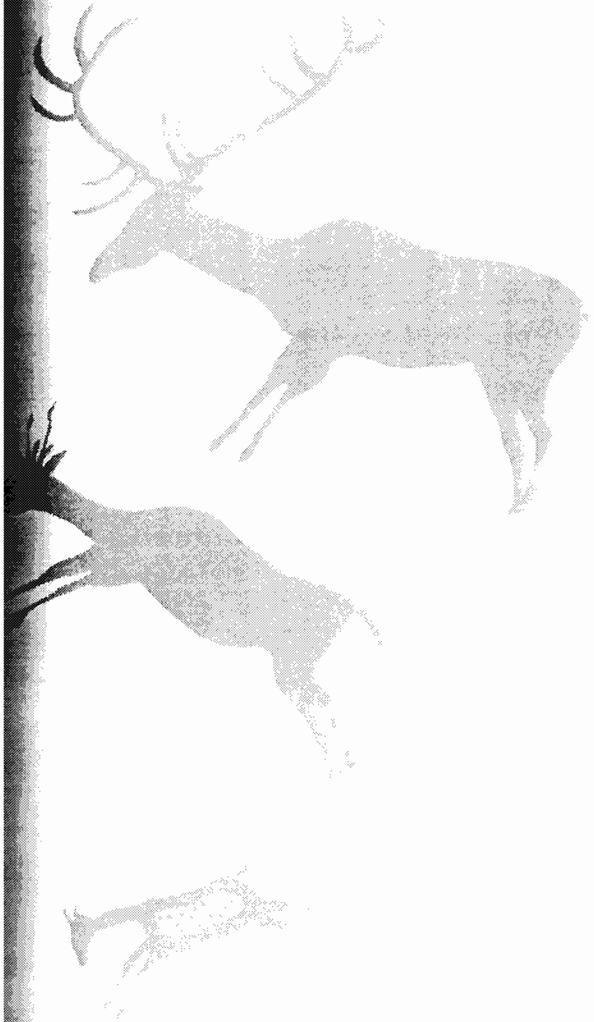
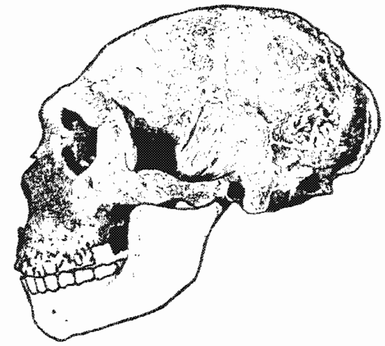
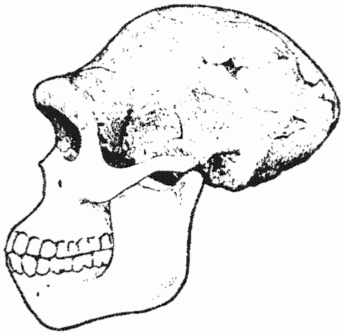
Canadian Journal of Anthropology
Revue Canadienne d'Anthropologie

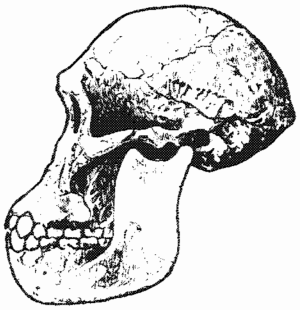
olume 3, Number 2, Spring 1983

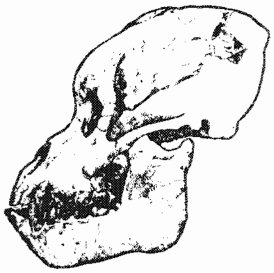
Human Evolution











Symposium on Human Evolution

Monday, October 4,
Tuesday, October 5, 1982
SUB Theatre
Students' Union Building
University of Alberta, Edmonton
Canada

EDITORIAL BOARD

The CANADIAN JOURNAL OF ANTHROPOLOGY/REVUE CANADIENNE D'ANTHROPOLOGIE is published twice yearly (spring and fall) by the Department of Anthropology at the University of Alberta.

MANUSCRIPTS

These should be addressed to the Editor, CJA/RCA, Department of Anthropology, University of Alberta, Edmonton, Alberta, Canada, T6G 2H4. Instructions for the preparation of manuscripts can be found on the inside back cover.

REPRINTS

Fifty (50) reprints will be provided *gratis* to each author or group of authors. Additional reprints will be available at a cost to be determined.

SUBSCRIPTIONS

Please make cheques payable to: Canadian Journal of Anthropology. (Canadian Funds in Canada; U.S. Funds for all other countries)

Individual: $15 per volume
Institutional: $30 per volume

Complete back file sets are available for continuing subscribers. Prices of back volumes and individual issues available on request.

ADVERTISEMENTS

Information can be obtained by writing to The Editor.

RICHARD FRUCHT MEMORIAL ESSAY PRIZE

The CJA/RCA will award an annual prize in memory of Professor Richard Frucht for an essay on the general topic of historical materialism. While no strict limitations will be placed on the specific area, preference will be given to essays which cover aspects of the following topics which were central to Professor Frucht's scholarly interests: political economy of the nation-state; rural masses and political movements; post slave society in the New World; historical materialism in anthropological theory.

The value of the prize will be $100 for students or $50 for non-students and the winning essay will be published in the CJA/RCA.

Essays should be no more than 5,000 words long and must reach the Editor by the 1st of January. They should conform to the style outlined in the "Notes to Contributors".

ISSN-0706-4845

Canadian Journal of Anthropology
Revue Canadienne d'Anthropologie

Volume 3:2
1983

PROCEEDINGS
of
A Symposium
on
HUMAN EVOLUTION

Editor
G.H. Sperber
University of Alberta
Edmonton

Published for
THE UNIVERSITY OF ALBERTA
by
THE CANADIAN JOURNAL OF ANTHROPOLOGY

Canadian Journal of Anthropology
Revue Canadienne d'Anthropologie

TABLE OF CONTENTS

Volume 3:2

PROCEEDINGS

of

A Symposium

on

HUMAN EVOLUTION

Held at the University of Alberta
Edmonton, October 4/5th 1982
in Commemoration of the University's 75th Anniversary

Editor
G.H. Sperber
University of Alberta
Edmonton

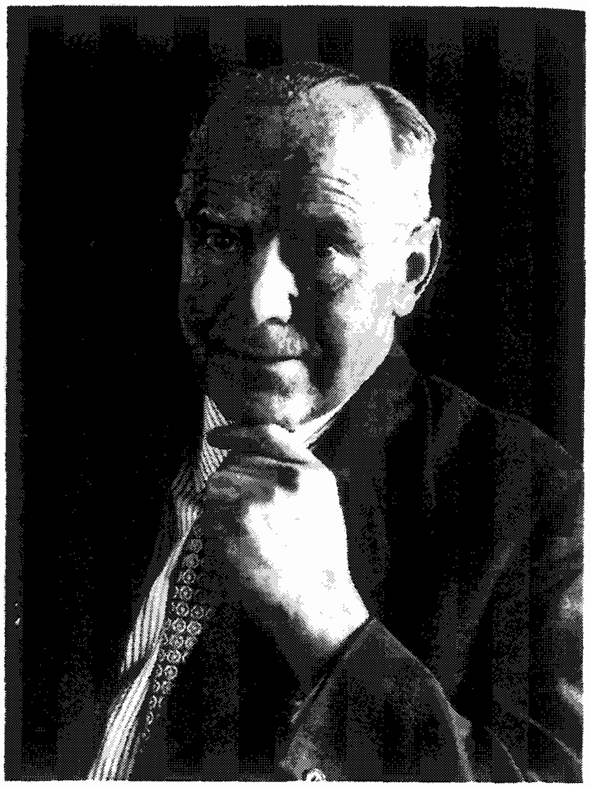
Published for

THE UNIVERSITY OF ALBERTA

by

THE CANADIAN JOURNAL OF ANTHROPOLOGY

1983



Dedicated to

RAYMOND ARTHUR DART

Professor Emeritus of Anatomy
University of the Witwatersrand

Discoverer of *Australopithecus*

on his Ninetieth Birthday

4 February 1983

Raymond Arthur Dart

Professor Raymond Dart was born in Brisbane, Australia on 4 February 1893 and was educated at schools in Queensland and at the Universities of Queensland and Sydney. After graduating B.Sc (Hon.) in 1913, he became a medical student at Sydney University. In 1915 he was awarded the M.Sc. and, in 1917, the M.B. Ch.M. (Hon.) of Sydney, which year saw him a demonstrator in anatomy.

Enlisted in the Australian Army Medical Corps, Dart served in England and France in 1918-1919. On demobilization he became senior demonstrator in anatomy under Professor (later Sir) Grafton Elliot Smith at University College, London. Elliot Smith, with his strong emphasis on the nervous system and its role in primate evolution, was another major influence in Dart's life. When the Rockefeller Foundation established its Fellowships program, Dart and his fellow-Australian anatomist, Joseph Shellshear, were the first two Rockefeller Fellows (1920-1921). Dart spent most of his American visit under Robert J. Terry in the Anatomy Department of Washington University, St. Louis, Missouri. Within a year of returning to University College, Dart was on his way to take up the Chair of Anatomy at the University of Witwatersrand, Johannesburg. Dart held the Chair from 1923 to 1958 and also served as Dean of the Medical Faculty for 18 years.

Some years after he retired from the Chair, when he was 70, he was appointed a Visiting Professor in the Institute for the Achievement of Human Potential at Philadelphia and ever since he has spent 6 months a year there in this capacity, even including his 90th year!

Dart's initial research contributions were in comparative neuro-anatomy and neuro-embryology, and a generation of protégés followed. He was interested in the peoples of Africa, and originated the concept that the Khoisan (Bushman-Hottentot) peoples of southern Africa were descended from an earlier population he called the 'Boskop race' (after the fossil human cranium found at Boskop near Potchefstroom, Transvaal, in 1913).

Dart's name will forever be associated with the discovery of the Taung skull and his prescient recognition of its significance. At a time when discoveries in Java and China led to the view that Asia had cradled mankind, there fell into Dart's hands in November 1924 a cache of fossil bones encased in hard calcified breccia. They had been recovered from a dolomitic limestone cave at Taung between Kimberley and Mafeking, on the edge of the Kalahari Desert. At that stage the only fossilized apes to have been found in Africa had come from much further north. Dart spent six weeks working on one of the specimens, the partly exposed natural endocranial cast of which had immediately struck him as being too large for a baboon. He laid bare the superbly preserved skull and 'brain-cast' of a child of perhaps five years of age. Although the endocranial cast was no bigger than that of an ape of comparable age, it showed a number of man-like features; so did the teeth, especially the small canines. In 1925 Dart published an account of the skull and proposed to make the creature the type-specimen of a new genus and species *Australopithecus africanus* ('southern ape of Africa'). He recognized it as a higher primate that was not a pongid (or member of the ape family): in its departures from the ape's structure, it had moved decidedly in a human direction, despite its ape-sized brain. He even demonstrated that the head must have been held on a virtually upright spine.

The claims of the 32-year old Dart received almost universal hostility. Nor did it help him to remind his colleagues that in 1871 Charles Darwin had predicted such ancestral forms to be more likely found in Africa than anywhere else. For a quarter of a century the place of *Australopithecus* was in dispute; but Dart stuck to his guns, and later adult specimens were found by Robert Broom at Sterkfontein. Sir Wilfred Le Gros Clark of Oxford vindicated Dart's claims by demonstrating not merely that the South African higher primates were *not apes*, but that they were members of the hominids or family of men, a view later widely-accepted.

Dart himself, his students and staff were responsible for finding another cave site containing australopithecine fossils, namely Makapansgat in Northern Transvaal. Long before such finds of very early hominids had started emerging from East Africa, Dart had been responsible for a remarkable series of fresh advances: *(i)* he had corroborated Darwin's old prediction that Africa would prove to have cradled mankind; *(ii)* he had forced upon a reluctant world the realization that a creature with a brain no bigger than that of a modern ape (recent man's brain-size is thrice that of an ape) could none the less show signs of moving in the human direction; *(iii)* he had shown that the principle of *mosaic* evolution had applied to these early claimants to human ancestry, that is, that some parts of the body (e.g., the teeth and the postural mechanism) had hominized in advance of other parts; and *(iv)* he had shown that the particular pattern of mosaicism shown by *Australopithecus* was totally at variance with that prognosticated by Dart's old mentor, Elliot Smith, who had strongly held that brain enlargement must have been in the vanguard of hominization: instead, in the *Australopithecus* brain enlargement was not evident, whereas dental and postural hominization were!

Dart's appreciation and interpretation of the hominid-like traits of *Australopithecus* represent the single most important breakthrough in paleoanthropology of the 20th century, and he lived to see his early claims vindicated. His claim that the australopthicines had used as tools the bones, horns and teeth of the animals they are presumed to have eaten was, however, strenuously resisted by most paleoanthropologists. Some believe that in this concept Dart had made another seminal contribution to the understanding of early stages of the hominization process.

With acknowledgements to the *South African Medical Journal* (63: 339).

SYMPOSIUM ON HUMAN EVOLUTION

FOREWORD BY THE CHAIRMAN OF THE ORGANIZING COMMITTEE

The celebration of anniversaries, be they birthdays or jubilees, is a ritual indulged in to demarcate the continuous passage of time in quanta that are comprehensible to our limited lifespans. Such occasions allow for the recognition of the achievements of individuals and institutions, and the attainment of the University of Alberta's 75th year in 1982 coincides most propitiously with the centennial of the death of Charles Darwin.

This coincidental set of events in 1982 led to the University of Alberta's 75th anniversary committee choosing "Human Evolution" as a topic for one of the several symposia arranged in celebration of its commemoration.

The quest for human origins is such an intrinsically fascinating pursuit that it forms the basis of myths, beliefs, folklore and faiths that in turn become organized into religions and the search for "roots." Science has now injected its realities into gaining understanding of our origins, and it is a story that is now rapidly unfolding in many disciplines of study. With this currency of controversy and topicality in mind, the organizing committee arranged an international symposium to take place in Edmonton at the University of Alberta in October 1982. I am fortunate in having had the cooperation of a willing committee, and I am particularly indebted to Dr. David Lubell of the Department of Anthropology of the University of Alberta who co-convened this symposium with me. I also wish to express my appreciation to Mr. Douglas Burns and Mr. Brian Silzer of the University's Administration for their superb organizational assistance.

Invited to participate were scientists acquainted with field work in the continents and countries producing the most prolific evidence of the origins of mankind, viz., Africa, and Asia, and specifically Kenya, South Africa, China and Indonesia. Further diversity was sought in bringing together geologists, anatomists, paleoanthropologists and behaviourists to create a melange of disciplines enabling a fascinating interaction of interpretations on the current state of understanding of human evolutionary processes.

A remarkable synthesis of ideas was achieved in correlating the anatomical, geologial and psychological frameworks in which mankind evolved. Immense eons of time and startling transformations of anatomical and cultural patterns were succinctly condensed by experts into components comprehensible to an avid professional and lay audience of some 600 persons. The proceedings of that symposium are published here for the enlightenment and enjoyment of a larger audience.

I am deeply indebted to those who contributed to the success of the symposium that in exploring the millions of years of man's prehistory added a significant passage to the University of Alberta's own history.

G.H. Sperber, Chairman of the Organizing Committee
75th Anniversary Symposia
University of Alberta
Edmonton
October 1982

GREETINGS FROM THE PRESIDENT
OF THE
UNIVERSITY OF ALBERTA

We at the University of Alberta are celebrating our 75th Anniversary during 1982-83. We have a golden opportunity to explore fields of endeavour that go beyond our normal range of research activities. We have planned, therefore, a number of symposia cutting across disciplines in the humanities and the sciences. I was particularly pleased when my colleague Geoffrey Sperber, who with a background in both anthropology and the health sciences, advocated the staging of a world class symposium on human evolution.

The 75th Anniversary Symposium Committee, under Dr. Sperber's chairmanship, devoted two years to the planning phase which resulted in our bringing together a number of international experts from diverse fields. For two brief days our university was the centre of learning on human evolution and I am pleased to have been involved in this outstanding conference which added much to the stature of the University of Alberta.

I extend my greetings and warmest congratulations to the organizers and participants who came from a number of countries, including Canada. I am very pleased that the proceedings of the symposium are now being published so that individuals who were unable to participate in Edmonton will benefit from the event.

Myer Horowitz
President

GREETINGS TO THE UNIVERSITY

Prof. PHILLIP TOBIAS

It is a privilege to bring greetings from Africa to the University of Alberta on its 75th Anniversary. The University of the Witwatersrand, Johannesburg, is this year celebrating its Diamond Jubilee: it was established as an independent University in 1922, though its precursors go back to the founding of the South African School of Mines in 1896. From it I convey felicitations to the University of Alberta. May the last quarter of its first century bring added lustre to its attainments in research and education, and to its service to the community and society.

Those of us who have been brought from far afield-from Asia, Africa and other parts of the North American continent-are grateful to the University of Alberta for its initiative in organising this Symposium and for inviting us to take part. Since anniversaries are always a time of looking back over the past, the theme of this Symposium, Human Evolution, is well chosen. In a manner of speaking, the roots of the University of Alberta go back not merely 75 years, but to the roots of all universities a few thousands of years ago; these in turn, to the roots of writing, several thousand years earlier; to the roots of human speech, human language, some hundreds of thousands of years before that; to the rudiments of human culture itself, in the depths of the Pleistocene epoch and even the dying days of the Pliocene epoch, between three and two million years ago! So your University can trace a longer history than you might have imagined: I wonder if that is why our Chairman, Professor Geoffrey Sperber, conceived the idea of such a symposium on this anniversary occasion. At any rate, whatever moved him to the notion, he is to be congratulated on convening this group and organising the symposium.

May the future of this University be as long and as remarkable as that ancient prehistory that lies behind it.

Prof. GLYNN ISAAC

I'd like to express my congratulations to the University of Alberta for its seventy-fifth anniversary, and I'd like to express my personal thanks for the invitation to be here, and to Professor Sperber and his colleagues for their superb efforts in organizing what is proving to be for me a very enjoyable and very informative symposium.

This is my first visit to Canada. I grew up in a sister dominion, as they both then were... and always had an interest in the country, a friendly feeling about it. Many of my student-day friends back in South Africa have now found their homes in Canada, so it's been a pleasure for me to visit the country properly at last and see something of it. I was in the field in Tanzania last week, and I feel a bit like one of the characters in the film "Quest for Fire"; for those of you who have seen it, they ranged rapidly from the Canadian north to the equatorial savannah. But I hope the resemblance between me and the characters in "Quest for Fire" has stopped there.

Prof. TEUKU JACOB

Commemoration of the 75th anniversary of the University of Alberta makes it appropriate to look back to the end of the 19th century, when a significant event occurred in the history of paleoanthropology. The Trinil hominid fossil was discovered in 1891. For Eugène Dubois, the discoverer, the find proved his hypothesis, fulfilled his ambition, and also changed the rest of his life. For paleoanthropology it was a milestone: *Pithecanthropus* was the first small-brained "missing link"; and it was the first fossil hominid found in the eastern part of the Old World.

It would be illuminating to describe very briefly the cultural environment surrounding this discovery. Indonesia at that time had not been entirely placed under Dutch rule. Wars were fought in Acheh at the northern end of Sumatra and in South Kalimantan (known in the West as South Borneo). In East Sumatra a tobacco crisis exploded and many plantations were closed. The population of Java and Madura in 1890 was about 180 per km^2 (it is now 690 per km^2). Coolies were being shipped from Java to New Caledonia and Surinam.

In the neighbourhood of Indonesia, Laos was invaded by the French in 1893, and the Philippines fell into the hands of the Americans in 1898. The Sino-Japanese war broke out in 1895.

Just like today, scientific discoveries continued to take place, regardless of the world situation. The electron, the ionosphere, argon, neon, krypton, xenon and actinium were discovered; followed by x-rays, uranium and radium. Theories were developed on aerodynamics, and light quanta. The diesel engine, the zeppelin, the automobile, the telegraph, and gillette razor blades were invented. The Nobel prize was instituted. Bacteriology underwent rapid development with many new bacteria being discovered. The first child was saved by diphtheria antitoxin in Berlin. Freud developed his psychoanalytic theory in 1895.

In Indonesia, the Dutch-Acheh war produced many cases of beri-beri among the Dutch troops recruited from other islands. Professors Winckel and Pekelharing, and their assistant, Eykman, were brought to Batavia to study it in 1886. Eventually the Eykman Institute of Pathology was established and Eykman received a Nobel prize in 1929 for his vitamin research. The Pasteur Institute was established in Batavia in 1891.

Haeckel had expounded his hypothesis on *Pithecanthropus alalus* in 1868. Dubois, strongly influenced by Haeckel as his assistant in anatomy and later physiology, though the East Indies would be a good place to search for the "missing link" in human evolution. The easiest way to go to this tropical archipelago seemed to be as an army physician, because the Dutch had lost many medical officers in their wars in Central Java in the early part of the 19th century, and later in Sumatra. Twenty-eight physicians had died in the first five years of the 30-year Dutch-Acheh war.

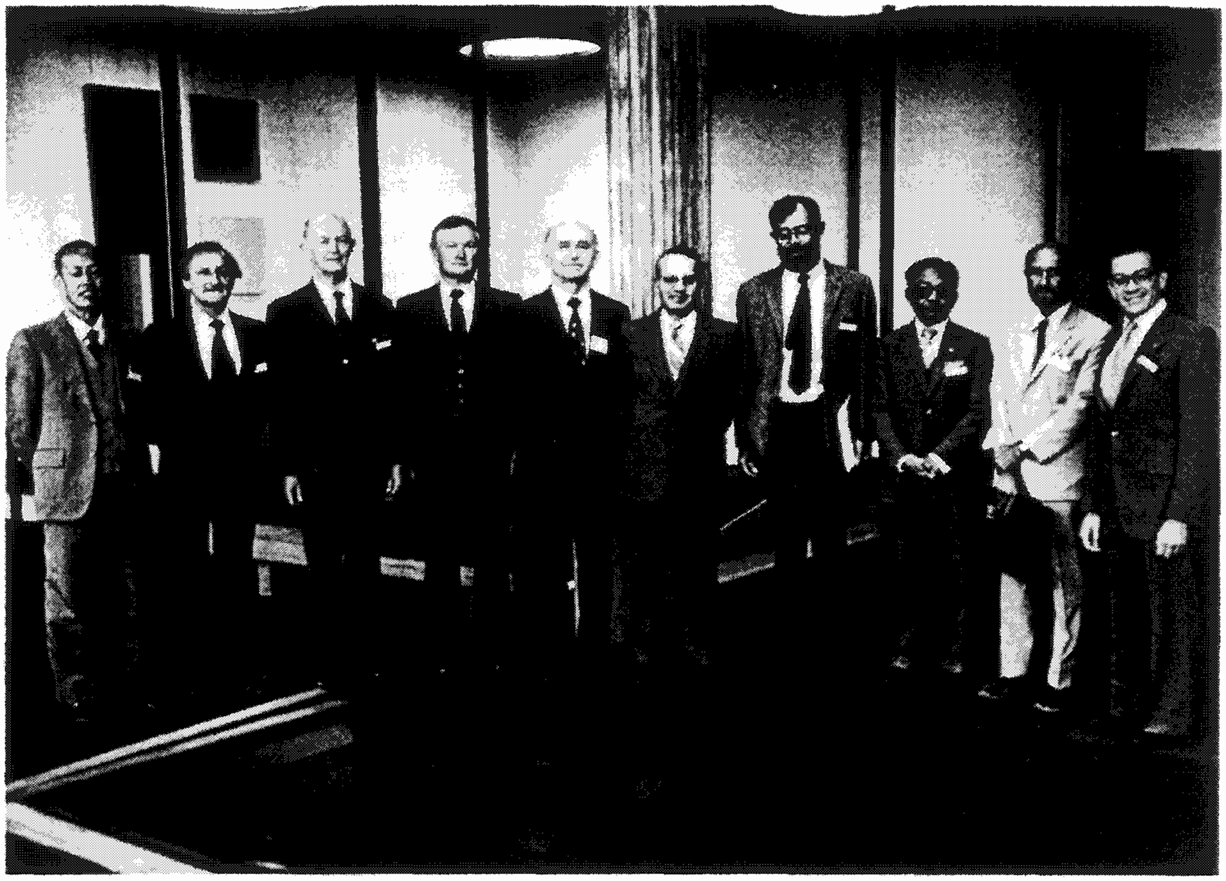
Eugène Dubois arrived in the East Indies in 1887 and soon he had convinced the authorities to allow him to do paleontological research in Sumatra with the help of 50 convicts as workers. Two years later the first Wajak skull was found in East Java, and the following year the first mandible of a hominid at Kedungbrubus.

Anthropological research (anthropology meant physical anthropology until the 1950s in Indonesia) had been carried out quite intensively in the East Indies. Research had been done on craniology and anthropology of isolated living populations, such as Negritos and Papuans. Almost all islands from Nias in the west to Irian (the term used by a local tribe to refer to New Guinea) in the east had been investigated. Great names were found among the investigators, including Virchow, de Quatrefages, Martin, Wallace, Mantegazza, and ten Kate.

This background to the truly amazing discovery at Trinil will, I hope, provide a framework of the world of thought and events which influenced the development of paleoanthropology and of Dubois himself as the main actor, a pioneer researcher on the evolution of man.

Henry Marshall Tory, another scientific visionary, became the first president of the University of Alberta in 1907, the year the German Academy of Science fielded an expedition to the Solo River in central Java in an unsuccessful attempt to confirm Dubois' discovery of *Pithecanthropus*. Confirmation came only thrity years later at Sangiran through the perseverance of the late G.H.R. von Koenigswald.

PARTICIPANTS IN THE SYMPOSIUM ON HUMAN EVOLUTION



From Left to Right: Prof. R. Wu, Prof. P. Tobias, Prof. B. Cooke, Mr. J. Schlosser (Chairman of the University of Alberta Board of Governors), Mr. P. Savaryn (Chancellor), Dr. M. Horowitz (President), Prof. R. Holloway, Prof. T. Jacob, Prof. G. Isaac, Prof. G. Sperber

Symposiasts

Dr. H.B.S. Cooke
B.A. (Hons.), M.A. (Cantab.), M.Sc., D.Sc. (Witwatersrand), F.R.S.S.Af.

Carnegie Professor of Geology (Emeritus), Dalhousie University, Halifax, N.S., Former Dean of the Faculty of Arts and Science, Dalhousie University, Former Reader in Stratigraphic Geology, University of the Witwatersrand, Johannesburg, S. Africa, Former Principal Geologist and Field Advisor to University of California African Expedition in Egypt, Sudan, East Africa, South Africa and Mozambique. Past President of the South African Geographical Society, the South African Archaeological Society, the South African Association for the Advancement of Science. Canadian Centennial Medal Award. Author of numerous books and articles on geology and evolution.

Professor Phillip V. Tobias
M.B., B.Ch., Ph.D., D.Sc. (Witwatersrand), Hon. D.Sc. (Natal), F.R.S.S.Af., F.L.S. (London), F.R.A.I.

Dean of the Faculty of Medicine, Head of the Anatomy Department, Honorary Professor of Paleoanthropology, and Zoology, University of the Witwatersrand, Johannesburg. Former Visiting Professor, Cambridge University. Past President of the Royal Society of South Africa, S.Af. Archaeological Society, Institute for the Study of Man in Africa, and S.Af. Society for Quaternary Research. A prolific worker, his over 500 published articles and books include: *Man's Anatomy, Chromosomes Sex-Cells and Evolution, Olduvai Gorge* Vol. 2, *The Brain in Hominid Evolution* and *The Bushmen: Hunters and Herders of Southern Africa.* A Nobel Symposiast, Tory Lecturer to the University of Alberta in 1973, Eponymous Lecturer and invited participant in workshops, symposia and congresses in many parts of the world. British Association Medal, Rivers Memorial Medal, Senior Captain Scott Medal.

Professor Wu Rukang (Woo Ju-Kang)
M.A., Ph.D. (Washington)

Deputy Director and Research Professor, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China. President of the Chinese Anatomical Association. Former Professor of Anatomy, Dalian Medical College. A Nobel Symposiast and author of numerous publications on Chinese Hominid Fossils.

Dr. Ralph Holloway
B.Sc. (New Mexico), Ph.D. (Calif.)

Chairman and Professor, Department of Anthropology, Columbia University, New York. Fellow of the American Association for the Advancement of Science. Fellow of the New York Academy of Science. Author of numerous publications in anthropology and hominid brain evolution.

Professor Teuku Jacob
M.S., M.D.

Rector and Professor of Anthropology, Gadjah Mada University, Yogyakarta, Indonesia. Former Dean of Medicine, Gadjah Mada University. Member of professional associations of anthropology, medicine, anatomy, human biology and archaeology. Editor of Indonesian Journal of Medical Sciences and Indonesian Journal of Bioanthropology. Nobel Symposiast and author of numerous publications in the field of human evolution.

Prof. Glynn Ll. Isaac
B.Sc. (Cape Town), B.A., Ph.D. (Cantab.)

Professor of Anthropology, University of California, (Berkeley), Former Deputy Director, National Museum of Kenya, Former Visiting Professor at Australian National University and Harvard University. Fellow of the American Association for the Advancement of Science and California Academy of Science. Director of the Foundation for Research into the Origin of Man. A Nobel Symposiast. Author of numerous publications on geology and evolution.

Human Evolution: The Geological Framework

H.B.S COOKE
2133 154 St.
WHITE ROCK, British Columbia V4A 4S5

Abstract: Fossil remains of fossil man are rare and normally only exist where burial by sediment takes place before disintegration occurs. This is most readily accomplished in low-lying basins where lakes are fed by streams carrying sediment in suspension, or in floodplain areas adjoining meandering streams; transport damage and sorting may occur. Caves also provide sheltered environments and are valued sources of hominid remains. Deep caverns and fissures have acted as traps for bone accumulation and can preserve material of greater antiquity than is possible in open caves; the South African australopithecine deposits and Zhoukoudian Locality 1 are examples. Each hominid specimen must be carefully dated, both relative to the entombing deposit and in terms of chronometric age in order to provide a sound basis for developing theories about evolutionary pathways. The paleomagnetic time scale now offers a valuable aid in dating and correlation on a global scale, but it still needs to be supported by faunal and chronometric dating if reliable conclusions are to be made.

In Europe the glacial-interglacial chronology has formed the main basis for dating but there is still disagreement on the correlations even within Europe. An attempt is made to summarize the estimates of possible ages for the principal hominids. In East Africa the occurrence of thick deposits rich in fossils and containing volcanic materials suitable for radiometric dating has yielded a well-founded chronology, supported by paleomagnetic data. The South African australopithecine deposits can be correlated approximately by faunal comparison with the "standard" East African sequence. The important hominid deposits of Indonesia are not yet very firmly dated but new paleomagnetic and radiometric studies are in progress. In China the glacial sequence has been established and related with the loess sequence, and there is some paleomagnetic control. The principal hominids can be placed in this stratigraphic scheme. The outlook for future work is good.

Résumé: Les restes fossilisés des premiers humains sont plutôt rares et n'existent que lorsque les ossements ont été enterrés avant qu'ils ne se désintègrent. Ces conditions se retrouvent le plus souvent dans les bassins peu élevés dont les lacs sont alimentés par des cours d'eau porteurs de sédiments en suspension, ou encore sur les plaines alluviales côtoyant les méandres de ces cours d'eau. Les conditions hydrauliques entraînent parfois dommages et réassortiment des os. On retrouve aussi des ossements d'hominides à l'intérieur de cavernes, celles-ci offrant une très grande protection contre les intempéries. Les cavernes ou fissures les plus profondes offrent, par leur protection accrue, la possibilité d'une plus grande accumulation d'ossements et, de ce fait, de trouvailles plus anciennes; les dépôts australopithèques en Afrique du Sud, et de Zhoukoudian, Localité 1, en sont un exemple. Des dates relatives (par rapport aux sédiments environnants) et chronométriques doivent être obtenues pour chacun des spécimens hominiens afin de pouvoir établir une base solide pour le développement de théories évolutionnaires. L'échelle paléomagnétique nous vient en aide en ce qui concerne datations et correlations à l'échelle globale, bien qu'elle n'ait pas encore été corroborée par datations fauniques ou chronométriques.

En Europe, la chronologie glaciale-interglaciale est utilisée comme étalon malgré le manque d'accord sur les correlations intra-européennes; les âges approximatifs des principales trouvailles hominides sont présentés brièvement. En Afrique de l'Est les dépôts riches en fossiles contiennent des matériaux volcaniques se prêtant aux datations radiométriques; ceux-ci nous ont livré une chronologie fiable, soutenue par l'évidence paléomagnétique. Les dates approximatives des dépôts australopithèques sud-africains sont obtenues par comparaison faunique avec la séquence est-africaine "type." Les importantes trouvailles hominides indonésiennes n'offrent pas encore de dates solides mais des études paléomagnétiques et radiométriques sont en cours. En Chine, la séquence glaciaire établie est reliée à la séquence loessique; à celles-ci vient s'ajouter un certain contrôle paléomagnétique. Les principales trouvailles hominides sont placées à l'intérieur de ce plan stratigraphique. Le futur semble prometteur.

Keywords: **Geology, Africa, Asia, hominid fossils, dating.**

Canadian Journal of Anthropology/Revue Canadienne d'Anthropologie—Vol. 3, No. 2, Spring 1983

INTRODUCTION

We humans seem to have a built-in curiosity about our ancestry that extends beyond the limits of our personal genealogical trees to a thirst for knowledge of the origins of man himself.[1] Indeed this curiosity has led to the development of many fascinating myths and legends that are reflected in the traditions of peoples in all parts of our planet, sometimes so deeply ingrained in their beliefs that alternative hypotheses were deemed unacceptable. It is a mere twelve decades since the revolution in thought that followed publication of Thomas Huxley's "Man's Place in Nature" (1863) and only eleven since the appearance of Charles Darwin's "The Descent of Man" (1871). At that time, although some remains had been found at a few sites in Europe, the only significant human fossils known were the skullcap and skeletal fragments from the Neander valley in Germany (1856) and the remarkable skulls and associated skeletons of five individuals from the Cro-Magnon cave in the south of France (1868). Today these remains are generally recognized as representing two varieties of our own species — Neanderthal Man or *Homo sapiens neanderthalensis* and Cro-Magnon Man, *Homo sapiens sapiens*, both of whom lived during the last glacial stage of the Pleistocene Period or "Great Ice Age."

The study of the actual skeletal remains of early man is the task of the physical anthropologist, who must obviously be well versed in human anatomy and familiar with the ranges of variability that are encountered in living populations of man. However, he must also be knowledgeable about the anatomy of the great apes and other primates with which man shares many anatomical, physiological and behavioural resemblances. Thus, evaluation of the characteristics of the fossil remains themselves is essentially a zoological problem. Yet any particular specimen represents only an instant in geological time and if we are to make meaningful comparisons between specimens it is essential that we place each find as accurately as possible into a common time frame, for only then are we entitled to formulate sound theories about the evolutionary pathways that may have been followed. Dating of the sediments is not solely the task of the geologist but calls also for the skills of the paleontologist, geophysicist, geochemist, palynologist and others. Nor is dating the only product of a multidisciplinary attack, for the deposits can yield much information about the environmental setting and even about the way of life of our remote relatives. Thus the bones themselves tell only part of the story.

PRESERVATION OF HOMINID FOSSILS

Fossil remains of man are rare and it would seem that the farther back in time we go, the rarer the discoveries become. There are probably several reasons for this. When a land animal dies in the open its remains are soon attacked by scavengers which scatter the bones and may even destroy them. What survives the scavengers is bleached by the sun and rotted by the rain. So if the bones are to have a reasonable chance of survival they must be protected in some way, more especially through rapid burial by sediment. This is most readily accomplished in low-lying basins, where lakes are fed by streams carrying sediment in suspension or in the flood plain areas adjoining meandering streams. Animals sometimes become trapped in the boggy borders of lakes and the bones of their skeletons may then remain associated to provide paleontological treasure, but man was probably too intelligent to be trapped in this manner so associated skeletons are extremely rare until deliberate burial of the dead became customary. Very commonly, the remains that we find buried in riverine or lacustrine deposits were transported by flowing water for some distance and they may thus be broken or show signs of damage. Even after burial in such an "open site," the bones may still be destroyed by percolating ground water, especially in areas where the water is rendered acid by forest debris. Indeed, the forest environment is an exceptionally poor one for preservation of bone and the fossil record is distorted by under-representation of forest dwellers. On the other hand, the presence of alkalis or lime in the soil helps to prevent solution of buried bone and one useful source of alkaline material can be volcanic dust, thus favouring preservation in volcanic regions provided, of course, that the volcanic activity does not destroy the deposits!

Another type of environment favourable for the preservation of animal bones is to be found in caves and fissures, especially in limestone regions. Caverns are formed by solution of the limestone in the upper part of the saturated zone, or groundwater. As regional erosion slowly lowers the landscape and deepens the valleys, the groundwater table sinks and the caverns are drained, but dripstones (such as stalactites and stalagmites) are deposited on the walls of the cavern by percolating water. Rainwater passing downwards from the surface dissolves the limestone along planes of weakness so that chimneys, or "avens", develop and eventually open to the surface. At this stage soil and surface debris begin to wash into the fissures and build up deposits on the cavern floor, often to be subsequently cemented into a hard "breccia" by percolating lime-charged water. The fissures are commonly concealed by bushes, or even trees, and unwary animals fall into the natural trap so that their bones accumulate on the cave floor, entombed by further falls of debris. Sometimes the head of the aven may provide a rock shelter or den for animals and their bones and the bones of their prey ultimately find their way into the deeper cavern. Erosion of the surface continues and at different stages more avens open, or the existing ones enlarge, and the roof of the original cavern becomes thinner and thinner until it is gone and the cave deposits themselves are exposed on the surface.

Apart from such deep caves, which fortunately preserve material of considerable antiquity for us to examine, surface caves of all kinds provide convenient shelters that have been used as dens, not only by animals but also by man. The cave floor is continuously covered with dust and dirt carried in by wind, water and the occupants, leaving a layered sequence in which we search eagerly for the ancient garbage that helped to build up the deposits. Such shallow caves are eventually destroyed by erosion so that few of the ones known today are of antiquity comparable to those of the deeper caverns, but they are very valuable sources of material and information.

Thus we see that the geological environments suitable for the preservation of remains of early man are very limited. The best conditions are probably represented by the "closed" environments offered by rock shelters, surface caves and subsurface caverns, although in the latter case the depositional mechanisms may lead to complex stratigraphic situations that can be difficult to interpret. Each individual cave deposit represents a discrete and isolated entity, usually covering a rather limited span of geological time — sometimes even a single catastrophic event — so that correlation between different caves and the determination of relative ages are difficult. By way of compensation for these difficulties, the fossils themselves are normally very well preserved.

The "open" sites are usually associated with fluviatile, lacustrine or volcanic environments, or occasionally with delta or lagoonal marine settings. Individual sites may be of very limited extent, leading to the same problems of correlation that we find with caves, but quite often the fossil-bearing areas occur as parts of a laterally extensive deposit and within a stratigraphic succession that represents a significant span of geological time. Such spatially and temporally extensive deposits are particularly valuable in establishing successive changes in the faunas and also in providing a reference framework for correlation. When such stratal sequences also include volcanic ash or lava horizons that can be used for radiometric dating, the situation is almost ideal but, alas, is also rare.

Although human fossils do occasionally occur in splendid isolation, they are normally associated in some way with animal fossils that can be identified and employed as an aid in correlation between scattered sites, or in the construction of a "synthetic" sequence by interweaving the data from many sites with overlapping faunas and ages. However, the associated fossils are also of considerable interest in providing information both about the conditions of deposition of the deposit itself and about the ecological environment prevailing at the time. The study of death assemblages — now known as "taphonomy" — is a fresh and expanding field that is beginning to explain some former puzzles. It is also proving very useful in directing field geologists into seeking out the particular depositional facies that appear to be most promising for yielding fossils; indeed "prospecting" for particularly suitable sedimentary environments is already productive. Taphonomic studies also provide a basis for trying to evaluate what components of the total spectrum of animals normally inhabiting an area actually find their way into the fossil assemblages. This is an important element in attempts to evaluate the paleoecology and paleoënvironment and may provide clues to the dietary preferences and habits of early man (see, for example, Behrensmeyer and Hill 1980, Brain 1981). Environmental interpretation in turn, is assisted by the collection and evaluation of fossil pollens, beetles or other invertebrates, coprolites, chemical studies of fossil soils, and so on. Thus very careful geological fieldwork is now an essential part of the search for early man and a fossil divorced from its context loses a great deal of its potential value for complete interpretation.

GEOLOGICAL TIME

The point in time where the line leading to man separated from that leading to the great apes is still a mystery and, although studies of biochemical and cellular factors suggest that the branching took place only 6 to 8 mya, it is to the fossil record that we must look for definitive evidence of what actually occurred. It is very important that each relevant fossil should be carefully dated. The problem has been well analysed and discussed by Oakley (1953, 1966), who recognized two main classes of dating, namely "Relative Dating" and "Chronometric Dating." Relative dating places an event with reference to some other event in a time sequence and represents the stratigraphical age of a specimen or of a geological formation. Oakley suggested a hierarchy of relative datings, R.1 being the age relation between the specimen and its containing deposit or associated fossils, R.2 the stage in the local or regional stratigraphic sequence to which the fossil-bearing horizon can be referred, R.3 the inferred position of that stage in terms of wide scale, or world, stratigraphy, and R.4 the geological age of a specimen inferred indirectly from the morphology. The R.1 dating is fundamental if we are to avoid being misled by intrusive burial or by derivation through erosion of an earlier horizon. It was R.1 dating that unmasked the Piltdown fraud. In the earlier days of paleoanthropology, before so much attention was paid to proper dating, R.4 type arguments were used to recognize "primitive" characters as "early" and "advanced" characters as "late," which is not necessarily true. However, R.4 dating can be used with some precision for correlation in cases where fossil mammals are abundant and were changing rapidly through time and where the changes can be calibrated or controlled from a thick sequence of well-dated strata. The South African australopithecine cave deposits are largely dated in this way by comparison with the excellent sequences now known from East Africa.

Chronometric dating (sometimes called "Absolute" dating) relies on actual assessment or measurement of the age in years and again Oakley (1953, 1966) has suggested a useful hierarchy. A.1 involves direct dating of the specimen, for example by measuring the carbon 14-radioactivity of the bone itself. A relatively new technique is the estimation of the degree of racemization of amino acids in organic tissue, but the accuracy of the method is dependent on assumptions about the thermal history of the deposit and the results are not always reliable. A.2 dating is derived from direct determination by physical measurements of the age of the sediments containing the fossil. The most important techniques are the radioactivity of carbon-14 in charcoal or shell for deposits younger than 50,000 years or, for older beds, the radioactive decay of potassium to produce argon in minerals that crystallize

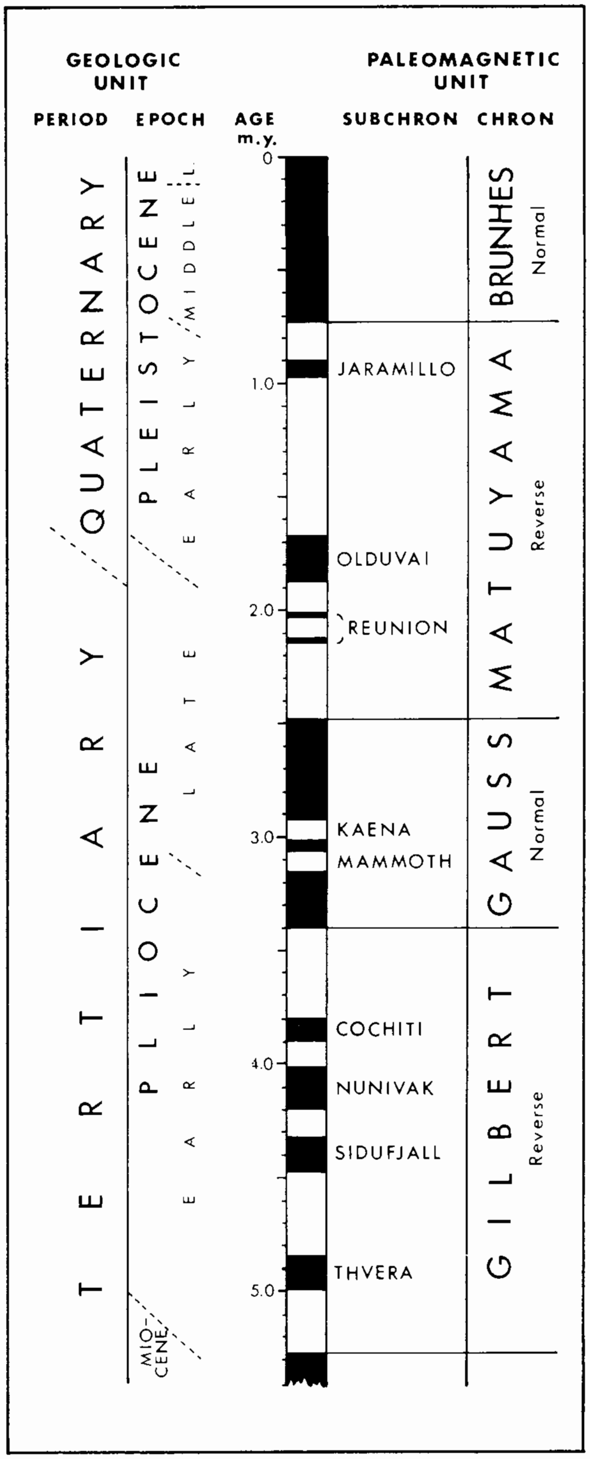


Figure 1. The paleomagnetic time scale for the past 5 million years. The ages for the boundaries are those of Mankinen and Dalrymple (1979).

in lavas or are ejected as volcanic ash falls (tuffs). Other methods, such as fission track dating of zircons, or other suitable grains occurring in ash falls are sometimes valuable and there are also other methods such as uranium series dating, the hydration of obsidian, or the thermoluminescence of quartz grains, that have limited applications. A.3 dating involves correlation of the fossil-bearing horizon with another deposit whose actual age has been determined by A.1 or A.2 methods. Geochemical characteristics of volcanic ash layers are proving increasingly important for confirming or amending age determinations in some areas. A.4 dating involves making estimates of age on the basis of some theoretical consideration, such as the matching of climatic fluctuations observed in the strata with astronomically derived curves for effective solar radiation, or matching terrestrial glacial/interglacial episodes with the marine paleotemperature or oxygen isotope record.

A relatively new technique of particular importance for the last few million years of geological time is paleomagnetic stratigraphy. As molten lavas cool and crystallize, magnetizable minerals in them acquire and retain a direction of polarity parallel to the lines of force of the Earth's magnetic field at that time. By measuring the polarity in lavas from many parts of the world, especially in areas like Iceland and Hawaii, and by dating the lavas by the K/Ar method, it is possible to study the behaviour of the Earth's magnetic field through time. It is found that the direction of polarity remains stable for long periods and then, quite suddenly, reverses itself and again remains stable in the new direction. The ages at which the geomagnetic inversions occur can be defined quite narrowly from the K/Ar ages and a reversal time scale can be constructed to fit all the data. When the field was directed towards the north rotational pole of the Earth, as at present, the field is said to be "normal," and when it is directed towards the south pole it is "reversed." Figure 1 shows the geomagnetic polarity time scale for the past 5 million years, using the revised determinations of Mankinen and Dalrymple (1979). The longer periods of general stability are called "Polarity Epochs" or "Chrons" but within them are shorter episodes, termed "Polarity Events" or "Subchrons" (Cox, Doell and Dalrymple 1964). The net result is a sequence of normal and reversed episodes that is unique and forms a "fingerprint" with which the sequence of changes in other sections can be compared. As the process is a global one, the reversal episodes are synchronous in all parts of the Earth.

Fortunately, sediments can also acquire the appropriate magnetic imprint and use of the polarity time scale has revolutionized the interpretation of ocean floor cores, where sedimentation is usually more or less continuous so that the sequence can be traced back through time and the epoch and event boundaries identified with a high degree of probability. In terrestrial sequences, continuous deposition is very unusual and unfortunately there is no identifying characteristic in the magnetic signals themselves that differentiates one reversal episode from another; it is only the pattern presented by a succession of reversals that makes the "fingerprint" matching possible. Accordingly, in terrestrial sequences it is necessary to obtain at least one approximate date somewhere within the span of the magnetic measurements in order to facilitate proper matching with the paleomagnetic time scale. Even then some ambiguity may remain. However, where good matching can be achieved, the reversal boundaries carry with them a very accurate date and this makes possible reliable age determination even in the absence of radioactive isotopes or other sources of A.1 or A.2 chronometric dating. So, while inherently an A.3 or A.4 method, it can achieve A.2 quality results in favourable circumstances. The geomagnetic polarity time scale is now commonly shown along with a radiometric age scale in charts of Pliocene-Pleistocene events, although this does not always mean that paleomagnetic data have been used in the allocation of stratigraphic units to their places in the time scale.

STRATIGRAPHY AND CHRONOLOGY OF HOMINID SITES

It is impossible in less space than a major volume to attempt to evaluate the geological setting and age estimates of all the known hominid specimens; the reader must be directed to other sources for this information. Oakley (1966) presented a most useful comprehensive tabulation of all the then-known specimens, together with their date of discovery, an estimate of the stratigraphic age, the chronometric age (if any), and categorization of the status of the age determination on his "A" scale. Day (1977) has provided a short summary of the geological setting and dating estimates for the most important fossil hominids, including useful references for additional data. The whole problem of dating hominid remains is discussed in a volume edited by Bishop and Miller (1972) in which Isaac has included a valuable critical appraisal of localities and dates associated with archaeological occurrences. This volume also includes an appendix with charts showing the rather limited chronometric dating controls for fossil hominids known at that time, which were exclusively African. A comprehensive volume focused on the middle part of the Pleistocene, edited by Butzer and Isaac (1975) also includes an appendix setting out in tabular form the estimated ages for most of the major hominid fossils of the past 2 million years, drawing particular attention to the range of uncertainty regarding those age estimates. It is not proposed here to attempt to repeat these data, but it seems worthwhile to offer some general observations on the broad features of the geological framework in the major areas from which human fossils have come.

Europe

Although the existence of a former more extensive ice cover in Switzerland was realized in the 1820's and in other parts of Europe shortly thereafter, it was not until more than 25 years later that the existence of evidence for multiple glaciations was recognized. In 1909 Penck and Brückner established the classical sequence of four glacial periods in the Alps, naming them, from youngest to oldest, Würm, Riss, Mindel and Günz, to which were subsequently added two earlier and lesser glacial episodes named the Donau (Eberl 1930) and Biber (Schaefer 1956). North Germany was glaciated by a Scandinavian-centred ice sheet, and four glacial stages were named Weichsel (youngest), Warthe, Saale and Elster, but they do not match directly with the four main Alpine glaciations as the Warthe appears to be coupled closely with the Saale and the two together are regarded as representing phases of the Riss Glaciation of the Alps; the Günz equivalent is not recognized in the glaciated Scandinavian — North German region. Further study has led to the recognition of breaks (interstadials) within the major glaciations, thus dividing the glacial units into two or more stages, and it is now realized that the actual situation is much more complex than would be inferred from the simple "four glacial" concept. It is in some ways unfortunate that the Alpine terms of Penck and Brückner have been used very widely — even outside Europe — as if they had some magical global application. Indeed, intercorrelation between different parts of Europe is still far from settled and correlation with the four North American glaciations is a matter of debate.

The thick sedimentary sequence in the Netherlands is slowly becoming the standard reference section for European Pleistocene stratigraphy. The succession has been probed by large numbers of boreholes and twenty-four lithostratigraphic formations with proper stratotypes are recognized for the later Tertiary and Quaternary (Zagwijn and van Staalduinen 1975). Actual glacial deposits are rare in the Netherlands basin, although both the Elster and the Saale are represented. However, abundant pollens make it possible to estimate the prevailing climatic conditions and to construct a curve showing the changes through the almost unbroken sequence. No radiometric dates are available, but there are sufficient paleomagnetic data to provide good control. Figure 2 shows the results in simplified form (following Zagwijn 1975a, b). It is clear that the sequence is complex and that there is potential difficulty in distinguishing interglacials from interstadials. Other work, principally in eastern Europe, has shown that deposits of the silt material called *loess*, which is derived by wind deflation from unvegetated outwash plains or newly exposed till, can be divided into depositional units that are separated by soil-forming warmer intervals; there are nine such units within the 700,000 year time span of the Brunhes normal polarity epoch (Kukla 1970, 1975, 1977). This complexity of the climatic changes is borne out by the record from deep-sea cores, both from fluctuations in the ratios of warm and cold loving organisms (see Ruddimann and McIntyre 1973, 1976) and by the oxygen isotope record (Shackleton and Opdyke 1973, 1976).

There is not yet agreement on how the glaciation chronology, the loess stratigraphy and the deep sea record are to be reconciled. There is evidence that at least the Eemian interglacial was short (25-30,000 years) and some authorities consider the other interglacials also to be short, leading to the rather widely accepted chronology shown in Figure 3b. However, there is also some evidence to suggest that in certain regions, interstadials have been confused with interglacials — for example a so-called "Eemian" in some areas between the Warthe and Saale phases of the Saale Glaciation. Zagwijn (1975) compresses the later glacials and gives the "Cromerian" Complex a substantial range in time (Figure 2, Figure 3a) whereas other authorities would restrict it. A compromise time scale is shown in Figure 3c. It may be expected that these different interpretations would affect the "absolute" ages assigned to the European fossil hominids but in fact it is only the earlier ones that are significantly affected, as will be seen in Table 1. Of course, other chronologies would give different results but the dates given in Table 1 probably reflect reasonable limiting ages.

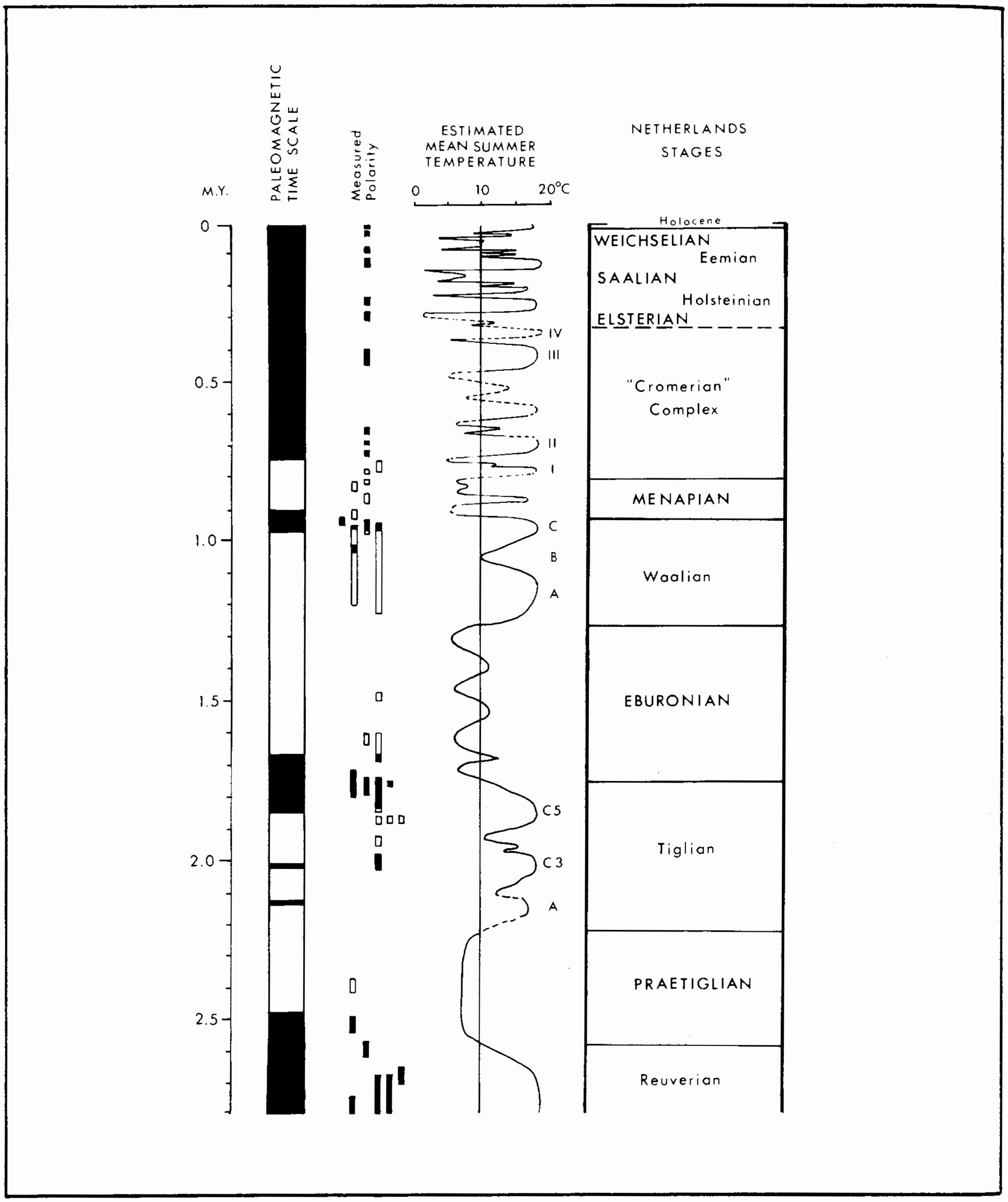


Figure 2. Climato-stratigraphic subdivision of the Quaternary in the Netherlands, showing the application of paleomagnetic data for age control of the sequence. The curve shows fluctuations in the mean summer temperature as deduced from pollen data. (Slightly modified from Zagwijn, 1975a,b). The names of the cold stages are indicated in CAPITALS and warm, or interglacial, stages in lower case.

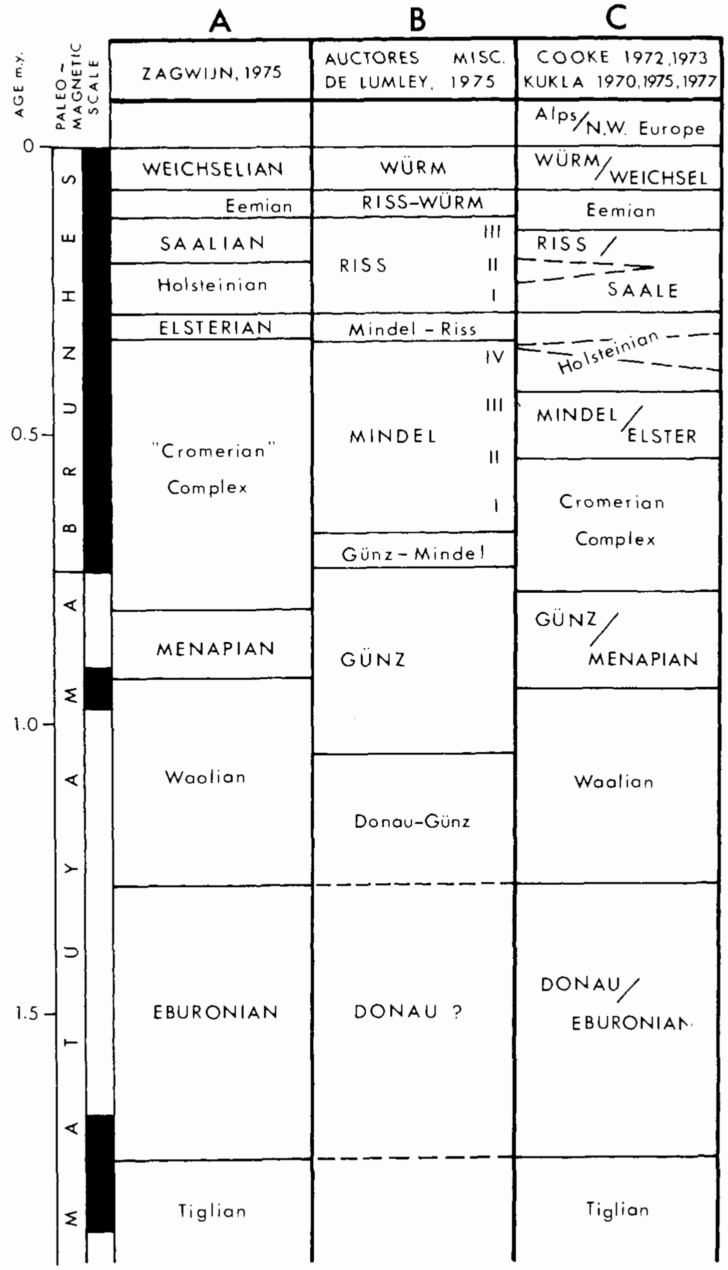


Figure 3. Three different interpretations of the climato-stratigraphic subdivision of the Quaternary sequence in Europe. A follows Zagwijn (1975b), with great compression of the post-Cromerian. B represents the most widely used scheme of many European workers. C is an interpretation that takes more account of the loess stratigraphy but also suggests that there has been some confusion of interglacial and interstadial environments.

TABLE 1

Comparison of Age Estimates of European Hominids
According to Different Chronologies

FOSSIL	STRATIGRAPHIC AGE	ESTIMATED CHRONOMETRIC AGE		
		A	B	C
Cro-magnon	Last glaciation	<50,000	<50,000	<50,000
Neanderthal	Last glaciation	<75,000	<75,000	<75,000
Krapina	Late Eemian	c85,000	c85,000	c85,000
Fontéchevade	Eemian	c100,000	c100,000	c100,000
Steinheim	Eemian	c100,000	c100,000	c100,000
Arago	Early Riss	c180,000	c250,000	c250,000
Swanscombe	Late Holsteinian	c210,000	c300,000	c300,000
Mauer	Mindel Interstadial	c230,000	c480,000	c480,000
Vértesszöllös*	Mindel Interstadial	c280,000	c480,000	c480,000

* There is a thorium/uranium determination of >300,000 years (Cherdyntsev, et al. 1965) but is not generally considered reliable.

Africa

North Africa has yielded a fine jaw from Ternifine, Algeria, a partial cranium from Salé and both cranial and mandibular remains from Sidi Abderrahman in Morocco; all of these have *Homo erectus* affinities but are poorly dated, though probably belonging to the later part of the Middle Pleistocene. A few Neanderthal-like specimens have also come from Morocco and Libya and more modern forms from other localities. There is also a curious specimen from Yayo, Chad that may be attributed to *Homo*, perhaps *H. erectus*; its age is uncertain.

Sub-Saharan Africa has furnished a few skulls of neanderthaloid character, notably the skull and other fragments from Broken Hill (or Kabwe) in Zambia which some authorities separate from the neanderthals proper as an African race, *Homo sapiens rhodesiensis*. To this form are also ascribed the Saldanha (or Hopefield, or Elandsfontein) cranium and mandibular fragments from the southwestern tip of the continent, the Cave of Hearths mandible from the Transvaal, and from East Africa the two crania from Lake Eyassi, Tanzania. There are also a number of interesting remains apparently ancestral to the modern African races of man. Most of these specimens are of Upper Pleistocene age, but the Saldanha skull is probably Middle Pleistocene.

The more ancient hominid remains occur in two widely different settings, the South African cave breccias and the East African rift valley deposits. The latter are all essentially similar in origin, comprising sequences of fluviolacustrine sediments with occasional horizons of volcanic tuffs that may be dated radiometrically or by fission-track dating of zircons or of volcanic glass. The most famous is the deposit at Olduvai Gorge, Tanzania, where the skull of a robust australopithecine was found in 1959 (Olduvai Hominid 5) and a radiometric age of 1.75 million years (Leakey, Evernden and Curtis 1961) provided the first concrete evidence for the antiquity of the australopithecines. A number of other important discoveries of hominids have been made at various levels. The 100 m thick deposit ranges in time from 2.1 million years at the base of Bed I to 0.8-0.6 million years for Bed IV. Paleomagnetic observations support the radiometric dates and this is the type location for the "Olduvai Event" of the magnetic polarity time scale. The geology has been described in detail by Hay (1976). Immediately south of Olduvai there is an older deposit, the Laetoli (or Laetolil) beds, consisting largely of fine volcanic tuffs that yielded important hominid fossils dated at close to 3.6 million years (M.D. Leakey 1976) as well as well-preserved footprints of the hominids of this remote time (M.D. Leakey and Hay 1979, M.D. Leakey 1981).

Other important sequences are those of the Omo area of southwestern Ethiopia, where the 750m thick Shungura Formation is divided into alphabetically labelled members by volcanic tuff horizons, most of which have been well dated. Detailed paleomagnetic studies have led to slight adjustments of some of the dates with the result that it now provides an unusually well controlled sequence. The Basal unit has an age close to 3.5 million years and unit L is approximately 0.8 million years old. Hominid remains occur throughout, and the succession forms a valuable reference frame for correlation of other deposits. The Omo river delta discharges into the north end of Lake Turkana (formerly Lake Rudolf) and on the east side of the lake, over an area 40 to 50 km in radius around Koobi Fora, similar fluviolacustrine deposits have yielded numerous hominid fossils. Two major units were recognized, but recent revision of the stratigraphy (Brown and Cerling 1982) suggests that it should all be included under the name of the Koobi Fora Formation. The East Turkana sediments were about 475 m thick and cover a time range similar to that of the Omo, but there is an erosional gap in the middle of the sequence so that the equivalents of Shungura Members D, E and F seem to be generally missing

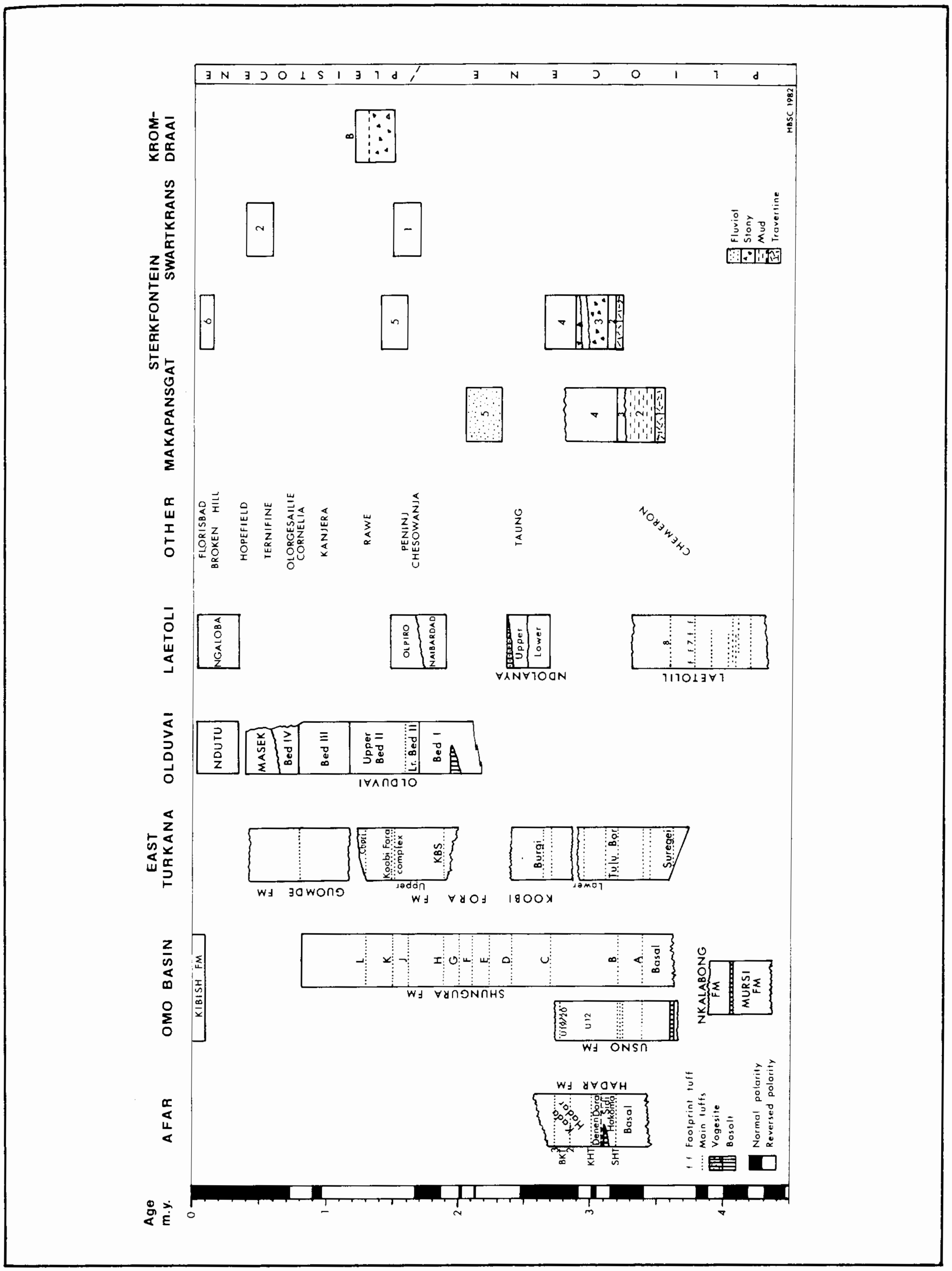


Figure 4. Tentative correlation of the main hominid-bearing stratigraphic units in Africa. The East African sequences are generally controlled by some radiometric dates and paleomagnetic records. The South African sites have no radiometric ages and are correlated mainly on faunal grounds by comparison with the East African sequence; there is some confirmatory paleomagnetic information but it can be ambiguous.

(Harris and White 1979, Cerling and Brown 1982). To the south of Lake Turkana, two restricted areas at Kanapoi and Lothagam have yielded fragmentary hominid fossils. Kanapoi is dated as close to 4 million years and Lothagam is estimated to be about 5.5-6.0 million years old.

In Ethiopia the Awash River drains northwards into the Afar depression. Exposed in the middle reaches of the valley is a thick sequence of deposits that covers a time range from the upper Miocene to the Upper Pleistocene and has yielded vertebrate fossils throughout, including some hominids (Taieb 1974, Kalb, et al. 1982a, b). Although work is proceeding on other portions of this very promising area, the most intensively studied section is that near Hadar, where the Hadar Formation has yielded a superb fauna, including valuable hominid material (Johanson, et al. 1982). The Hadar sequence is stated to range from about 4.0 to 2.7 million years (Johanson, et al. 1982) but there are problems with some of the data and the paleomagnetic records would accord better with a range nearer 3.5 million years at the base and a corrected radiometric age closer to 3.1 million years for the Kadada Moumou Basalt (Aronson, et al. 1977). In the upper part of the Middle Awash sequence, the Bodo Member of the Wehaieta Formation has yielded an archaic *Homo* cranium of probably Middle Pleistocene age. Tentative correlations are shown in Figure 4.

In South Africa the important australopithecine deposits are cave breccias resulting from the slumping of surface debris into ancient underground caverns, as was described above. Subsequent to their primary filling, the deposits have been subjected to erosion and new channels, fissures or cavities were sometimes developed within the earlier breccias so that breccias of different ages may be in contact (see Brain 1981). Erosion has generally removed most or all of the original roof so that the pinkish-brown breccias are exposed at the surface. Each site samples a different time span and correlation between the deposits relies on the faunal material. Comparison with the faunal sequence in East Africa suggests that the deposits of the Makapansgat Limeworks are probably close to 3.0 million years old while the Lower Breccia at Sterkfontein is slightly younger. Direct dating by radiometric or geochemical methods have been unavailing, but some paleomagnetic observations support the 3 million year age implied by the fauna (McFadden, et al. 1979). On similar faunal grounds, the Sterkfontein Extension site (Member 5) with its stone tools, is estimated to be only half as old. At Swartkrans there are two breccias with different faunas, Member 1 with a faunally estimated age of about 1.7 million years and Member 2 as perhaps only about 0.5 million years. At Kromdraai, the australopithecine breccia ("B") is estimated faunally to be about 1.5 million years old. The deposit at Taung, which furnished the type specimen of *Australopithecus africanus*, is poorly dated but may lie somewhere between the ages of Sterkfontein and Swartkrans 1, probably close to 2.0 - 2.5 million years.

Indonesia

The discovery of the "Java Ape-Man" at Trinil 90 years ago was a landmark in paleoanthropology and has been followed by further important finds of *Homo erectus* near Sangiran and also by the recovery of other material at Ngandong, generally termed "Solo Man." All these localities lie in the drainage basin of the Solo River in eastern Java (Djava) between Surakarta and Surabaya, while an isolated site at Perning, near Mojokerto, lies some distance from the Solo River about 40 kilometers west of Surabaya. Isolated finds have been made at Sambungmacan, 20 kilometers west of Trinil, and at Kedung Brubus, 100 kilometers east of Surakarta (Figure 5). A list of discoveries, in chronological order, has been given by Jacob (1976).

Java is part of an island arc system extending through Sumatra (Sumatera) and Timor, bordered on the south side by the deep Java Trench. It is a tectonically active belt and is marked by a line of young volcanoes. The geology has been described in some detail by Van Bemmelen (1949). The Southern Mountains of Java are built of volcanic rocks with interbedded marine sediments of Miocene age, injected by granitic intrusives. These rocks were uparched in the later Tertiary to form a chain of islands, while the area to the north (now the area of the Solo River drainage system) was a shallow platform in which Pliocene deposits were laid down. The Pliocene Kalibeng Formation consists of marls, clays and silts, with occasional horizons of volcanic tuff, and the uppermost part includes marine limestones. Increased volcanic activity is apparent at the base of the overlying Pucangan Formation as volcanic mudflow breccias (lahars) occur in some areas. The "typical" sediments of the Pucangan Formation are freshwater "black clays" suggesting deposition in a ponded lake, but there are localized fluviatile sections with vertebrate fossils and also some marine horizons suggesting that there were occasional short-lived connections with the sea; farther to the east the Pucangan Formation is represented largely by a marine facies. The relatively quiet deposition of the Pucangan Formation was suceeded by an influx of coarser debris so that the Kabuh Formation has some conglomerates but is largely made up of crossbedded sandstones and tuffaceous sandstones with plant remains and vertebrate fossils, although clays and silts also occur. The Kabuh Formation has furnished the bulk of the hominid remains. Rapid growth of the volcanoes, perhaps accompanied by regional uplift, is reflected in the Notopuro Formation, in which lahar flows and explosive volcanic breccias are prominent and mammalian fossils are only rarely preserved. The age of the Notopuro Formation is uncertain but it is generally believed to be Middle to Upper Pleistocene.

Fossil vertebrates occur sporadically in the Pliocene Beds in Western Java, where uplift seems to have begun earlier than in the eastern part of the country. Here two faunal units were distinguished, an earlier Tjidjulang Fauna and a later Kali Glagah Fauna, but they are virtually unknown in the Solo River basin. Both faunas have a Siva - Malayan aspect. In eastern

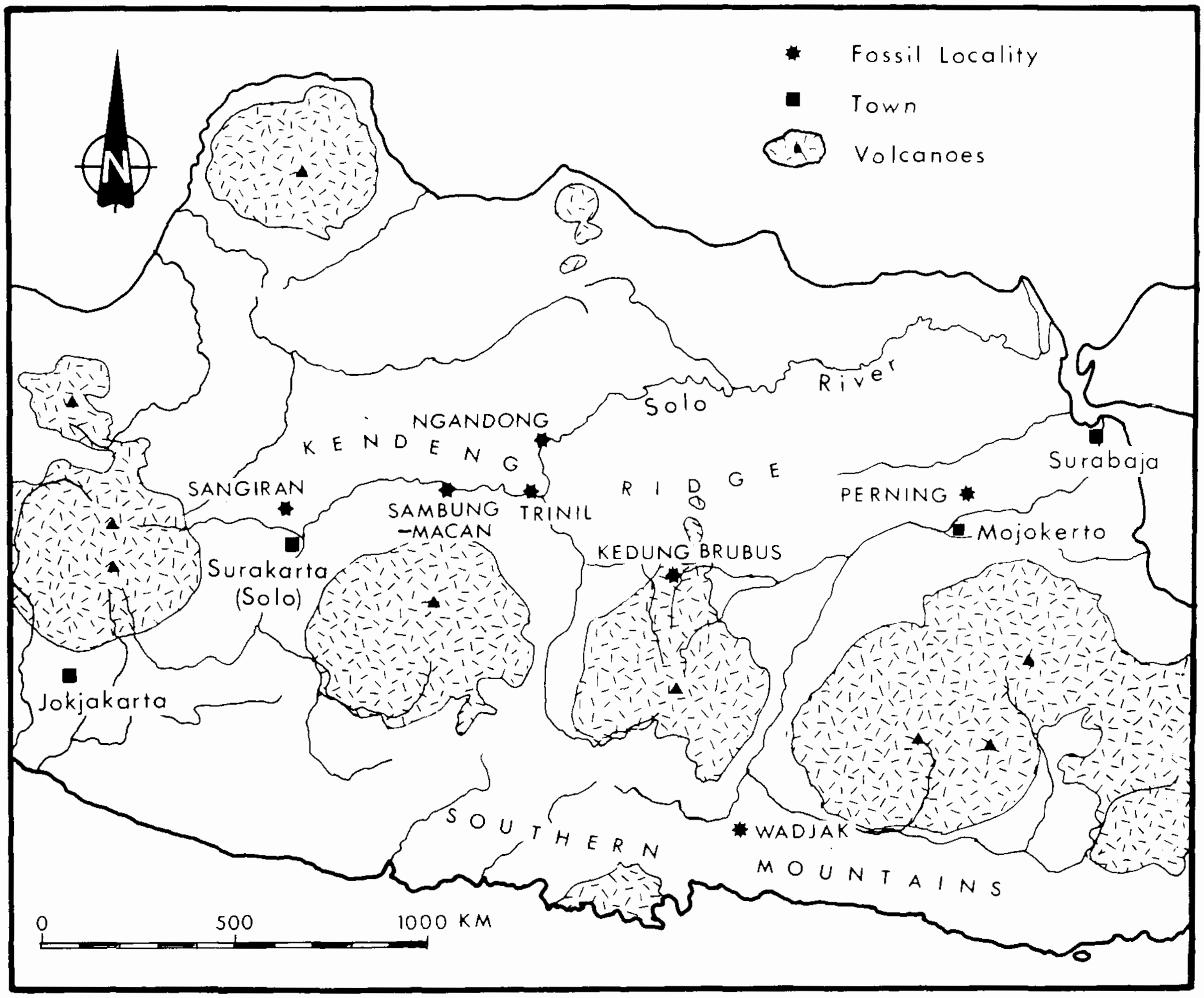


Figure 5. Simplified map of part of eastern Java to show the location of the principal hominid fossil sites.

Java, the Pucangan Formation contains a rich and varied fauna with some Siva - Malayan elements but with others showing a connection with the faunas of southern China. First recognized in the area around Mojokerto, it is distinguished at the Jetis (or Djetis) Fauna and has been recorded from the type area westwards as far as Surakarta. Fossils do not occur in the Pucangan beds at Trinil but there the Kubuh Formation contains a slightly different assemblage known as the Trinil Fauna, which has affinities with the *Stegodon - Ailuropoda* fauna of southern China. Von Koeningswald (1949) regarded the Jetis and Trinil faunas as distinct, placing the former as Early and the latter as Middle Pleistocene, but Hooijer (1951, 1962) denied the distinction and considered that both are probably Middle Pleistocene. Sartono, et al. (1981) report the discovery of some elements of the Trinil fauna in the upper volcanic facies of the Pucangan Formation, suggesting that the two faunas overlap and that there is need for re-investigation and possible revision. In any case, lateral facies changes probably diminish the value of the equation of the Formations to the faunal units.

The Formations described above underlie the upper reaches of the Solo River, which cuts into them, but successive phases of incision — probably controlled by tectonic events rather than by climate — have led to the development of river terraces on the flanks of the river. Only three were formally recognized and named the Ngandong, Low and Flood terraces respectively. More recent work has disclosed the existence of three earlier terraces, although they are rather obscured (Sartono 1976). The most important is the Ngandong terrace, about 20 m above the present river bed and, in the type area, only some 50 m above sea level. This terrace is the source of the fossil hominids collectively called "Solo Man." An abundant mammalian fauna occurs and constitutes the Ngandong Fauna of Von Koeningswald (1951), usually regarded as Upper Pleistocene but quite possibly ranging back into the Middle Pleistocene; some elements of this fauna have been found in the Notopuro beds. The hominid remains show clear evidence of river transport and it has been suggested by Santa Luca (1980) that they could have been derived by erosion from an earlier deposit and may not be contemporary with the mammalian fauna; this is an R1 dating problem that should be capable of testing by chemical or other means but is at present unresolved.

At Trinil the type material of *Homo erectus* came from the Kabuh beds exposed on the flanks of the river and not from the terrace gravels. The most important hominid site is the Sangiran area, north of Surakarta, where the fossiliferous deposits that are normally concealed beneath a blanket of Notopuro beds are well exposed as a result of tectonic upwarping to form the Sangiran Dome (Figure 6). A schematic cross-section in the northwestern part of the Sangiran dome, showing only the major facies, is shown in Figure 7A, following Semah, et al. (1981). The term "grenzbank" has been applied to a calcified conglomerate that forms a convenient marker horizon for the boundary between the Pucangan Formation and the Kabuh Formation. The relative positions of the homonid fossils from Sangiran are shown diagrammatically in Figure 7B, from Jacob (1980) but the thicknesses do not appear to be to scale.

A cranium of *Home erectus* and some stone artefacts were found at Sambungmacan, near the Solo River some twenty-five km west of Trinil, but the stratigraphy of the site is not clear (Sartono 1979). Jacob, et al. (1978) placed the fossil near the boundary between the Pucangan and Kabuh beds and suggested that the normal magnetic polarity might indicate an age of about 900,000 years and represent the Jaramillo Event. Sartono (1978), on the other hand, considers that both the Kabuh and the Pucangan are missing from the area and that the fossil-bearing deposit most likely represents the Ngandong Formation; this would place the paleomagnetic signal as within the Brunhes normal epoch.

Dating of the Pucagan-Kabuh succession is still unsatisfactory. A pumice from Sangiran sites 10 and 12 is reported to have a radiometric age of 830,000 years and tektites from the top of the Kabuh beds at Sangiran were dated at 710,000 years (Jacob 1975). Basalts from the Muriah volcanic complex some 80 km north of Trinil have been dated as close to 500,000 years (Von Koeningswald 1962, Evernden and Curtis 1965) and are said to be from volcanic breccias that contain a typical Trinil vertebrate fauna. There is thus quite a scatter in age estimates. Preliminary results of a paleomagnetic study are not definitive (Semah, et al. 1981) but give weak indications of a reversed polarity field through most of the Pucangan Formation, with a strong reversed signal in and near the diatomite zone (see Figure 7A). In contrast, the Kabuh beds show normal polarity, with the reversal not far from the contact with the Pucangan. While it is possible that this change is at the base of the Jaramillo event, it is equally likely that it represents the Brunhes/Matayuma transition with an age of 0.73 million years. The rather uncertain normal magnetization at the bottom of the Pucangan and top of the upper Kalibeng Formation might possibly represent the Olduvai event. This is not incompatible with the analysis by Siesser and Orchiston (1978) of forminifera in claystone attached to a mandible from the lower Pucangan beds, which they considered to be Pliocene with a minimum age of 1.6 million years.

The juvenile mandible from Kedung Brubus, found in 1890, and the child skull discovered in 1936 at Perning, near Mojokerto, although widely separated in space, have both been regarded as about 1.9 million years old on the basis of age determinations on pumice from Mojokerto and on andesite from Kedung Brubus (Jacob 1975). Doubt has been cast on the stratigraphic assignment of the Mojokerto skull, which Sartono, et al. (1981) consider belongs to the Kabuh Formation rather than the Pucangan, but the problem is far from resolved and the age of these specimens must await further field studies. On balance it seems likely that the Pucangan Formation may range from about 1.9 m.y. to perhaps 0.9 m.y., while the Kabuh Formation covers a rather short time span from 0.9 - 0.7 m.y. More detailed studies of the paleomagnetic record and the ages of the interbedded tuffs are required.

China

China has approximately the same area as Canada but covers a range of latitude equivalent to that from Jamaica to Hudson Bay, thus having a tropical climate in the south and an arctic one in the north. More than half of the total area is part of the vast plateau system of Inner Asia, culminating in the high tableland of Tibet (Xizang), most of which is over 3500 metres above sea level and includes the highest point on earth, Mt Everest (Jolmo Lungma - 8848m). The Tibetan ranges are continued southwards in the Hingduan and Daxne mountains of the Yunnan and western provinces, although at lesser elevations, and these ranges merge into an extensive highland area that occupies the southeastern part of the country. The two great rivers of China, the Yellow River (Huang) and the Yangtze (Chang) originate in the Tibetan highlands and are flanked by extensive lowlands in their lower reaches. The only other extensive lowland area is the Manchurian Plain (or Northeast Plain) lying between the Korean highlands in the east and the Da Hinggan range on the west. The Qin Ling range lies on the south side of the Yellow River and forms a convenient line of separation between the well watered and forested southeastern part of the country and the semi-desert and desert of the Mongolian plateau and the Gobi desert to the north and the Taklimakan desert of the Tarim basin to the west. The northwestern desert region includes the Turpan depression, 154 metres below sea level in strong contrast to the elevated Tibetan Plateau.

The complex mountain and basin structure is the consequence of the geologically recent (Miocene) collision of the Indian Plate and the Asian Plate and the whole region is still tectonically and seismically active. The several scattered and isolated basins were receptacles for Cenozoic sediments, often coarse grained at the base and becoming finer in the upper part, when lacustrine conditions prevailed. Widespread uplift and tectonic activity in the Miocene was followed by another cycle of deposition but through much of China erosion has been a dominant feature. The pioneer work of Lee (1939) and the classic syntheses of Teilhard de Chardin (1941) and Movius

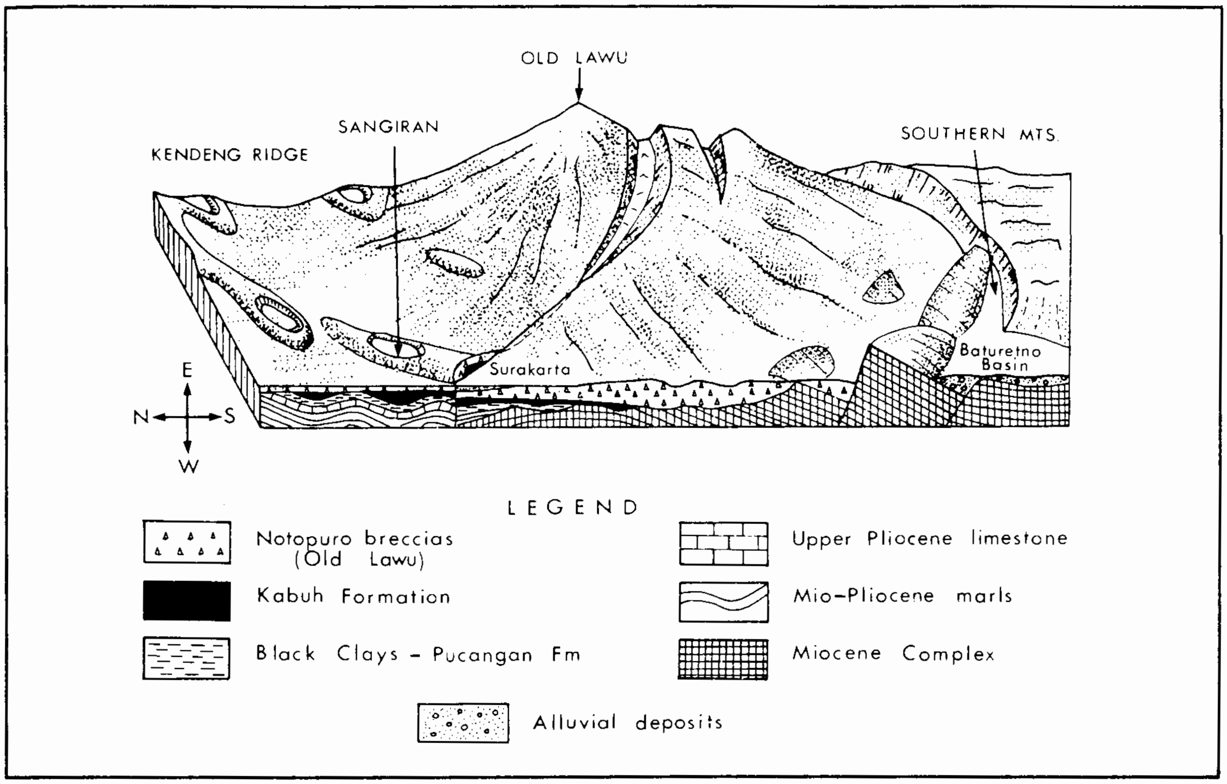


Figure 6. Schematic diagram to show the development of the Sangiran dome at the end of the Notopuro period, leading to exposure of the Kabuh and earlier deposits that are normally concealed by a blanket of Notopuro breccias (modified after van Bemmelen, 1949).

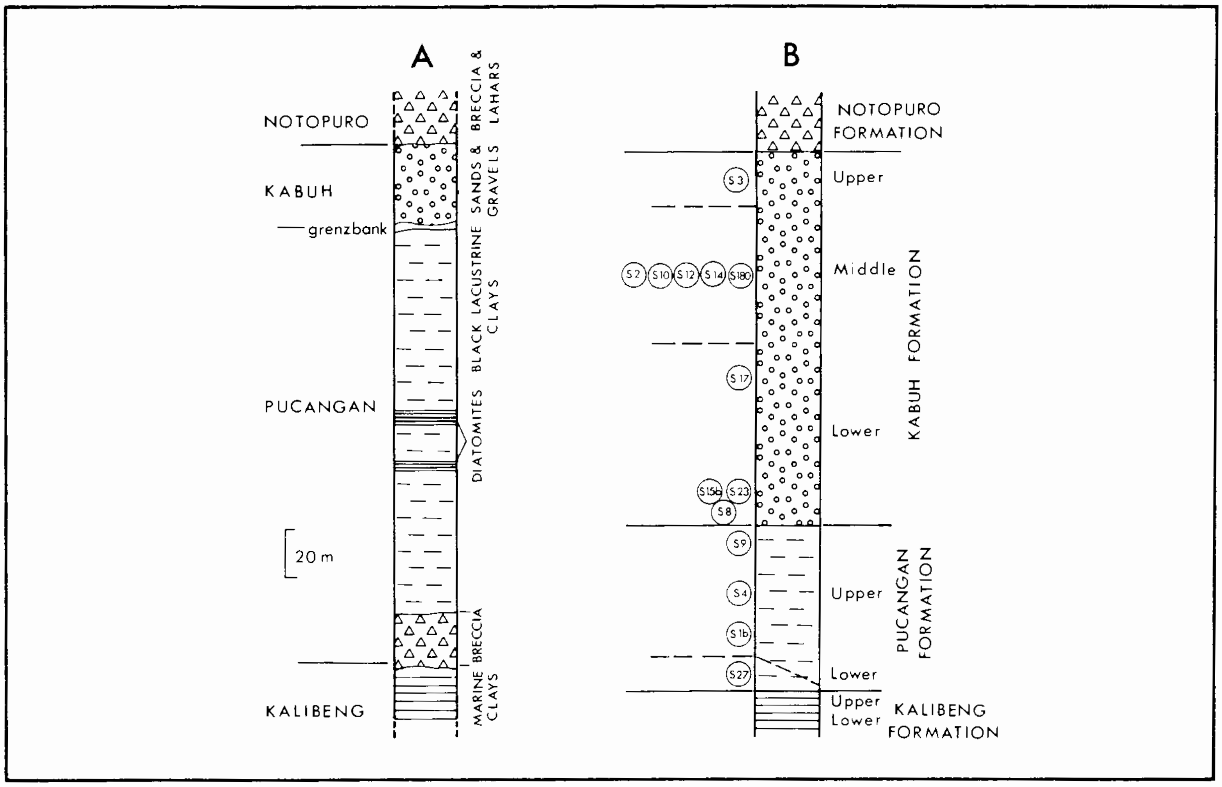


Figure 7. A. Schematic cross-section in the northwestern part of the Sangiran dome, showing the relative thickness of the major facies (after Sémah et al. 1981). B. Relative positions of the hominid fossils from the Sangiran area, not to scale (from Jacob 1980). The specimen numbers are shown in the circles.

(1948) led to recognition in the Yellow River basin of a succession of sedimentary cycles, separated by erosion intervals and the following scheme was developed:

Young alluvium

Panchiao erosion

Malan Loess

Chingshui erosion

Upper Sanmenian - Choukoutienian Reddish Clay

Huangshui erosion

Lower Sanmenian Red Clay (Nihowan Beds)

Fenho erosion

Pliocene Beds (including Red Clays with Hipparion)

The Nihowan fauna includes *Proboscihipparion, Equus sanmeniensis* and *Elephas planifrons* and is regarded as of Villafranchian age. The Upper Sanmenian fauna contains the same *Equus* species, lacks *Proboscihipparion* and has a more advanced elephant, *Elephas hysudricus*, regarded as Middle Pleistocene. The Malan loess is late Pleistocene, associated with *Equus hemionus* and *Elephas namadicus*. The classic areas are generally north of the Qin Ling range and correlation with the area to the south is complicated by the fact that North China and South China are different zoogeographic provinces (Pei 1957). In the south, the place of *Elephas* is generally taken by *Stegodon*, although *Elephas* may also occur, and *Ailuropoda* — the so-called "giant panda" — is often present, thus providing a link with Java and other parts of the Siva-Malayan geographic region. Li (1981) suggests that four sub-divisions may be recognized and other groupings of local faunas have been proposed (Ji 1982; Wang and Ouyang, 1982). A stratigraphic scheme of classification proposed by Liu, et al. (1964) provides the general framework now being followed by many Chinese workers and Liu's tables have been translated in a valuable survey by Chang (1977). Aigner (1972) has suggested faunal and climatic correlations with the European sequence. Useful data on recent views are also presented by Howells and Tsuchitani (1977).

Glaciers are found at present in the high Tibetan Plateau and in the Tian Shan mountains on the north side of the Tarim basin. During the Pleistocene these glaciers were more extensive but eastern Tibet and the adjoining highlands of Sichuan and northern Yunnan (much of which is over 4,000 metres above sea level) also harboured major glaciers and there is good evidence for glaciation in other highland areas (see Figure 8). In some valleys the ice descended as low as 3,000 metres and is even reported as extending below this level into the lower reaches of the Yangtze River. A number of separate glacial stages can be distinguished in eastern China and each is apparently associated with its own distinctive till deposits. Five glacial stages have been named the Hongya (oldest), Poyang, Taku, Lushan and Tali glaciations and there is also a phase of periglacial activity, called the Dongcheng, between the Hongya and the Poyang (see Sun, et al. 1981).

One of the effects of glacial activity is the production of large quantities of finely ground rock or mineral particles, often called "rock flour," and this material is carried away from the edge of the ice by meltwater. The finest fraction is removed by streams but the silty material is left on the outwash plains and is readily carried away by the wind to be deposited eventually somewhere downwind of the source as *loess*. Similar material can also be derived from desert areas where, as in the outwash plains of glaciated regions, there is no vegetation to bind the surface. China has received dust from both sources and loess covers more than three quarters of a million square kilometres, commonly 50 m thick and in places reaching as much as 500 m. The major area is in the basin of the Yellow River (Huang), which derives its name from the discolouration caused by the constant load of yellow loess that it carries. The Chinese loess is fully described by Liu and Chang (1962) and has been reviewed briefly by Brown (1977). The northern limit of the loess coincides remarkably well with the Great Wall and the southern margin is formed by the Qin Ling range. The "Loess Plateau" of eastern Gansu, central and northern Shaanxi and Shanxi is very fertile, as are also the loess areas of Henan and the redeposited loessic alluvial plains of the Yellow River basin. Three major phases of loess deposition are recognized, the Wucheng, Lishi, and Malan. The Wucheng loess is associated with the Nihowan fauna. Paleomagetism has furnished dating control for the loess sequences (Heller and Liu, 1982). A much simplified outline is presented here in Figure 9 to show the relative ages assigned to the glacial and loess stages and the relative positions of the principal hominid fossil remains.

The oldest hominid so far found consists of two incisors recovered in red clays at Yuanmou, 100 km northwest of Kunming in Yunnan Province, southwest China. The 650 m thick Yuanmou Formation is divided into four members and has a good mammalian fauna. There has been some disagreement about the environmental interpretation but Ji and Li (1979) have reinterpreted the fauna as representing a subtropical assemblage of early Pleistocene age. Paleomagnetic study of the Yuanmou Formation led to placement of the hominid fossils at 1.7 million years (see Atlas 1980). However, this assessment has been revised recently and the fossils are now placed at the Jaramillo Event with an estimated age of around 900,000 years BP (Wu Rukang, personal communication).

A skull cap from red clays at Gongwangling ("Lantian Man") near Xi'an in southern Shaanxi, has been placed by paleomagnetic dating between the Jaramillo Event and the base of the Brunhes (Ma, et al. 1978). The Lantian jawbone came from similar deposits near Chinjiawo village, about 30 km from the skull site and is assigned to the lower part of the Brunhes Normal paleomagnetic epoch. Faunal comparisons have been made by Ji (1980).

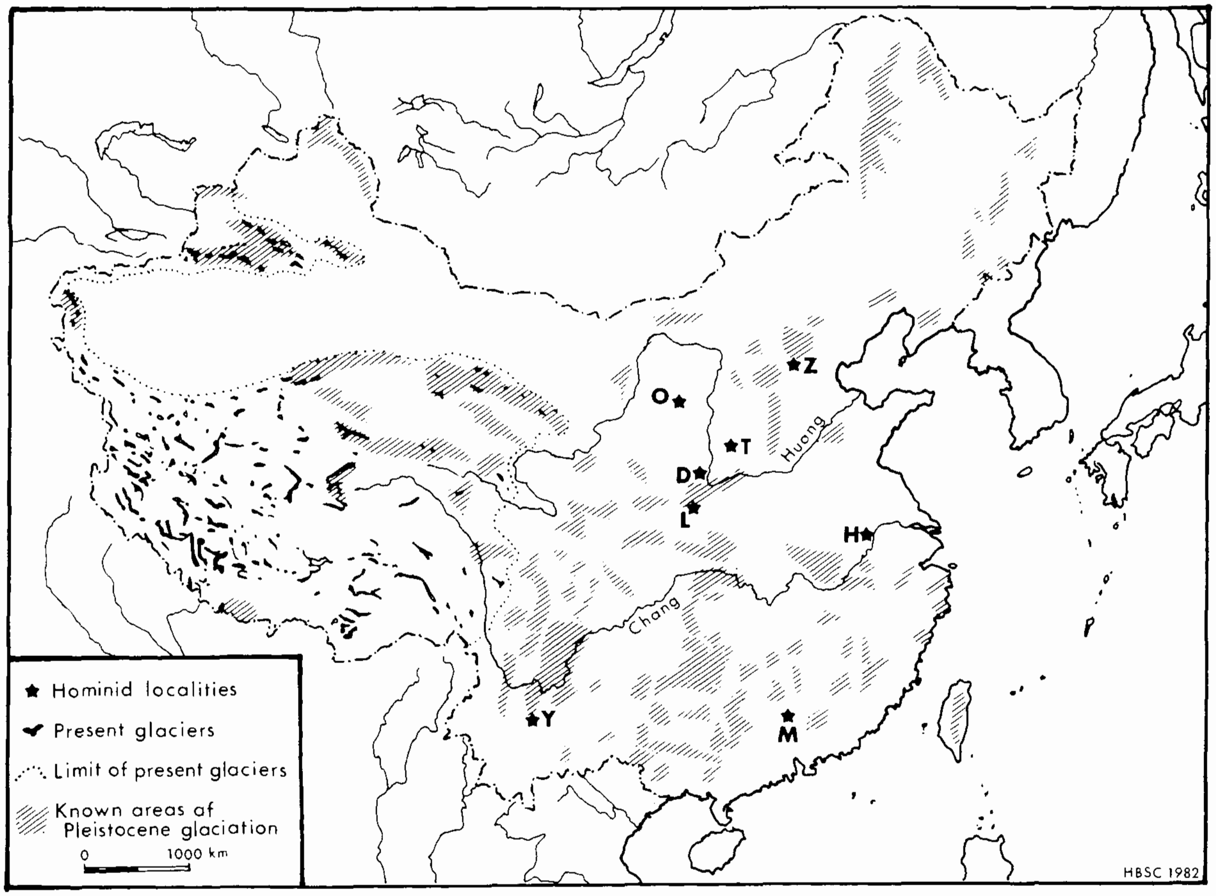


Figure 8. Sketch map showing the distribution of existing glaciers in China and the main areas affected by glaciers in the Pleistocene (after Sun, et al. 1981). The major hominid localities are shown by stars as follows: Y - Yuanmou; L - Lantian; Z - Zhoukoudian; H - Hexian; D - Dali, M - Maba; T - Dingcun; O - Ordos.

The most famous area for hominid fossils is near the village of Zhoukoudian (Choukoutien), some 45 km southwest of Beijing (Peking), where the Western Hills rise from the great North China Plain. The Ordovician limestones here contain many caves and fissure fillings and twenty-two localities have been found, although only a few have yielded hominid remains or artefacts. The most extensive is Locality 1 or the "Lower Cave," in Dragon Bone Hill, where the filling of a former cave measures 140 m in length (east-west) and 40 m in breadth at its widest part. The original cave roof collapsed into the deposits from time to time as erosion thinned it and the present site is essentially only the filling, as with the South African sites. The thickness of the accumulated deposit is more than 40 m and it has been divided into 13 stratigraphic units, numbered from top to bottom. The basal gravel and reddish silt includes glacially worn pebbles and pollens indicating a cold environment, most probably the terminal part of the Taku Glacial stage. The first stone tools are found just above the unit but no hominid remains occur with them. A sandy layer follows and is rich in hyena bones and coprolites, above which occur the first hominid fossils, which continue sporadically through the upper part of the breccia. Ash layers, burned seeds and bones attest to the use of fire. Climatic changes indicated by the fauna are discussed by Xu and Ouyang (1982), who deduce an alternation of colder and warmer stages through the sequence and suggest correlation with Kukla's (1975, 1977) loess cycles D, E, F. This is in agreement with the faunal correlations. Some of the other localities in the vicinity cover parts of the same time range as Locality 1 (Localities 2, 3, 13) but others are older (12,18) or younger (15, 22, 4, the latter connected to "New Cave" or Xindong Cave). Very much younger is the "Upper Cave," which is late Pleistocene and has yielded some fine hominid material as well as a radiocarbon date of 18,500 years BP.

An important discovery was made in 1980 in Longtan (Dragon-Pool) Cave at Hexian, Anhui Province, some 60 km southwest of Nanjing (Nanking). The cranium is almost complete and was the first *Homo erectus* skull to be found in South China. A rich mammalian fauna is distinctive and appears to correspond neither to the typical Zhoukoudian fauna of the north nor to the *Ailuropoda-Stegodon* fauna of South China (Huang, et al. 1982).

A nearly complete cranium, recently described by Wu (1981) as Dali Man is regarded as the earliest *Homo sapiens* and is dated as late Middle Pleistocene

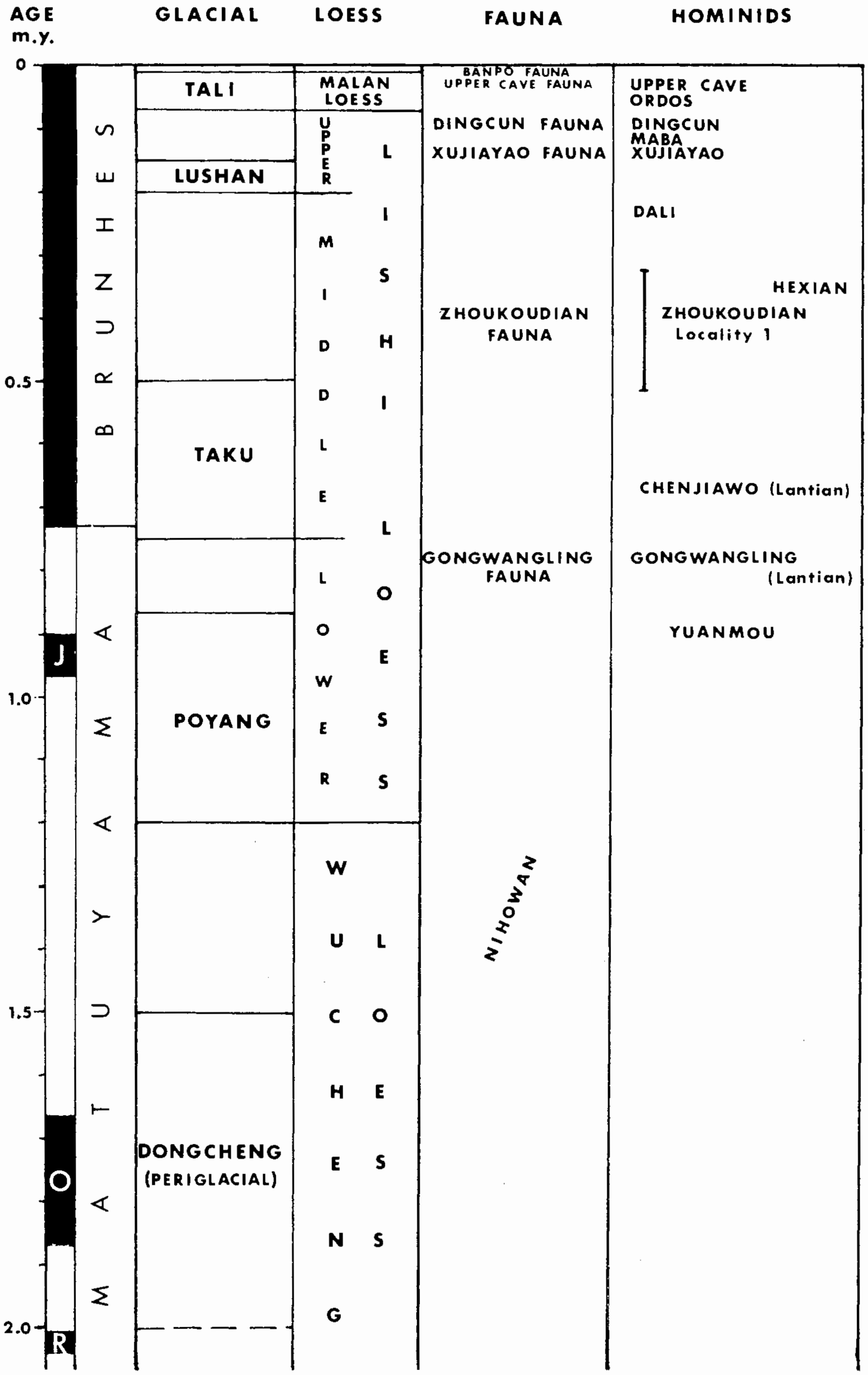


Figure 9. Simplified climato-stratigraphic scheme for China to show the relative positions of the main hominid occurrences.

(circa 0.15 - 0.2 m.y. BP). Maba Man is represented by an incomplete cranium from a cave deposit in Guangdong Province. The site of Dingcun (Ting-ts'un) comprises a lengthy stretch of alluvial sands and gravels, capped by loess, along the east bank of the Fen River in Shanxi Province and it has yielded more than 2,000 artifacts as well as three hominid teeth and a portion of parietal. The Ordos site in Inner Mongolia also consists of river terrace deposits and was the source of the first hominid find in China in 1922 (an incisor) but later yielded some cranial fragments, three limb bones and some stone implements. Like the material from the Upper Cave at Zhoukoudian, it represents a modern type of man, although not totally Mongoloid. Many sites of late Pleistocene age also occur, mainly in cave deposits.

CONCLUSION

Although in each of the regions discussed above it now seems possible to place the more important hominid fossils within a local relative chronology, there is still a considerable margin for error; for example the changes in age estimation for Yuanmou Man from 1.7 to 0.9 million years. The existence of this range of uncertainty must be recognized in the formulation of theories on the pathways of human evolution on a global scale. Great strides have been made in the past two decades but much work remains to be done by inter-disciplinary teams to firm-up the dating framework, as well as to provide further insight into the environments of the past.

NOTES

1. It is hoped that no offence will be taken by women at this conventional use of the masculine form which is employed for simplicity but is intended to embrace human males and females alike; who, after all, is interested in the ancestry of "personkind"?

REFERENCES CITED

Aigner, J.S.
1972 Relative dating of North Chinese faunal and cultural complexes. Arctic Anthropology 9(2): 36-79.

Aronson, J.L., T.J. Schmitt, R.C. Walter, M. Taieb, J.J. Tiercelin, D.C. Johanson, C.W. Naeser and A.E.M. Nairn.
1977 New geochronologic and paleomagnetic data for the hominid-bearing Hadar Formation of Ethiopia. Nature 267: 323-327. London.

Atlas Of Primitive Man in China.
1980 Compiled by Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences. Distributed by Van Nostrand Reinhold, New York. Beijing: Science Press.

Behrensmeyer, A.K. and A.P. Hill, (eds.)
1980 Fossils in the Making. Chicago: University of Chicago Press.

Bemmelen, R.W. Van.
1949 The Geology of Indonesia. Vol.1A. The Hague: Martinus Nijhoff.

Bishop, W.A. and J.A. Miller, (eds.)
1972 Calibration of Hominid Evolution. Edinburgh: Scottish Academic Press.

Brain, C.K.
1981 The Hunters or the Hunted? Chicago: University of Chicago Press.

Brown, F.H.
1977 Notes on Chinese Loess. *In*: W.W. Howells and P.J. Tsuchitani. Paleoanthropology in the People's Republic of China. National Academy of Sciences, Committee on Scholarly Communication with the People's Republic of China, Report No.4: 168-178. Washington, D.C.

Brown, F.H. and C.E. Cerling
1982 Stratigraphic significance of the Tulu Bor Tuff of the Koobi Fora Formation. Nature 299: 212-215. London.

Butzer, K.W. and G.Ll. Isaac, (eds.)
1975 After the Australopithecines. The Hague: Mouton.

Cerling, T.E. and F.H. Brown
1982 Tuffaceous marker horizons in the Koobi Fora region and the lower Omo valley. Nature 299: 216-221. London.

Chang, K.C.
1977 Chinese paleoanthropology. Annual Reviews of Anthropology, 1977 (6): 137-159.

Conroy, G.C., C.J. Jolly, D. Cramer and J.E. Kalb
1978 Newly discovered fossil hominid skull from the Afar depression, Ethiopia. Nature 276: 67-70. London.

Cox, A., R.R. Doell and G.B. Dalrymple
1964 Geomagnetic polarity epochs. Science 143: 351-352.

Day, M.H.
1977 Guide to Fossil Man. Third ed. Chicago: University of Chicago Press.

Eberl, B.
1930 Die Eiszietenvolge im nördlichen Alpenvorlander. Augsburg: Benno Filser.

Harris, J.M. and T.D. White
1977 Evolution of the Plio-Pleistocene African Suidae. Transactions of the American Philosophical Society 69(2):128 pp.

Hay, R.L.
1976 Geology of the Olduvai Gorge. Berkeley: University of California Press.

Heller, F. and Liu, T-s.
1982 Magnetostratigraphic dating of loess deposits in China. Nature 300: 431-433. London.

Hooijer, D.A.
1951 The Geological age of *Pithecanthropus, Meganthropus* and *Gigantopithecus*. American Journal of Physical Anthropology 9: 265-281.

1962 The Middle Pleistocene fauna of Java. *In*: G. Kurth. Evolution und Hominisation. pp. 108-111. Stuttgart: Gustav Fischer.

Howells, W.W. and P.J. Tsuchitani (eds.)
1977 Paleoanthropology in the People's Republic of China. National Academy of Sciences, Committee on Scholarly Communication with the People's Republic of China, Report No. 4. Washington, D.C.

Huang, W., D. Fang and X. Ye
1982 Preliminary study on the fossil hominid skull and fauna of Hexian, Anhui. Vertebrata PalAsiatica 20(3): 248-254 (in Chinese, English summary 255-256).

Isaac, G.Ll.
1972 Chronology and the tempo of cultural change during Pleistocene. *In*: W.W. Bishop and J.A. Miller (eds.), Calibration of Hominid Evolution. pp. 381-430. Edinburgh: Scottish Academic Press.

Jacob, T.
1975 Morphology and paleoecology of early man in Java. *In*: R.H. Tuttle (ed.), Paleoanthropology, Morphology and Paleoecology. pp. 311-325. The Hague: Mouton.

1980 The *Pithecanthropus* of Indonesia: phenotype, genetics and ecology. *In*: L-K. Königsson (ed.), Current Argument on Early Man. pp. 170-179. Oxford: Pergamon Press (for the Royal Swedish Academy of Sciences).

1981 Solo Man and Peking Man. *In*: B.A. Sigmon and J.S. Cybulski (eds.), *Homo erectus*: papers in honour of Davidson Black. pp. 87-104. Toronto: University of Toronto Press.

Jacob, T., R.P. Soejono, L.G. Freeman and F.H. Brown
1978 Stone tools from Mid-Pleistocene sediments in Java. Science 202: 885-887.

Ji, H-x.
1980 The subdivision of Quaternary mammalian faunas of Lantian district, Shaanxi. Vertebrata PalAsiatica 18(3): 220-227 (in Chinese, English summary 227-228).

Ji, H-x.
1982 The living environment of the Quaternary mammalian faunas in South China. Vertebrata PalAsiatica 20(2): 148-154 (in Chinese, English summary 154).

Ji, H-x., and Li, Y-x.
1979 Note on the living environment of Youanmou Man. Vertebrata PalAsiatica 17(4): 318-324 (in Chinese, English summary 324-326).

Johanson, D.C., M. Taieb and Y. Coppens
1982 Pliocene hominids from the Hadar Formation, Ethiopia (1973-1977): stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. American Journal of Physical Anthropology 57(4): 373-402.

Kalb, J.E., C.B. Wood, C. Smart, E.B. Oswald, A. Mabrete, S. Tebedge and P.E. Whitehead
1980 Preliminary geology and paleontology of the Bodo D'Ar hominid site, Afar, Ethiopia. Palaeogeography, Palaeoclimatology and Palaeoecology 30: 107-120.

Kalb, J.E., E.B. Oswald, S. Tebedge, A. Mebrate, E. Tola and D. Peak
1982a Geology and stratigraphy of Neogene deposits, Middle Awash Valley, Ethiopia. Nature 298: 17-25. London.

Kalb, J.E., C.J. Jolly, S. Tebedge, A. Mebrate, C. Smart, E.R. Oswald, P.E. Whitehead, C.B. Wood, T. Adefris and V. Rawn-Schatzinger
1982b Vertebrate faunas from the Awash Group, Middle Awash Valley, Afar, Ethiopia. Journal of Vertebrate Paleontology 2(2): 237-258.

Koenigswald, G.H.R. von.
1949 The discovery of early man in Java and southern China. *In*: W.W. Howells (ed.), Early Man in the Far East. Studies in Physical Anthropology, 1: 83-98. Philadelphia.

1951 Geology and paleontology. *In*: Fr. Weidenreich (ed.), Morphology of Solo Man. American Museum of Natural History, Anthropological Papers: 219-221.

1962 Das absolute Alter des *Pithecanthropus erectus* Dubois. *In*: G. Kurth (ed.), Evolution und Hominisation. pp. 112-119. Stuttgart: Gustav Fischer.

Kukla, G.J.
1970 Correlation between loesses and deep sea sediments. Geologiska Föreningen i Stockholm Förhandlingar 92: 148-180.

1975 Loess stratigraphy of Central Europe. *In*: K.W. Butzer and G.Ll. Isaac (eds.), After the Australopithecines. pp. 99-188. The Hague: Mouton.

1977 Pleistocene land-sea correlation. 1. Europe. Earth Science Reviews 13: 307-374.

Leakey, L.S.B., J.H. Evernden and G.H. Curtis
1961 The age of Bed I, Olduvai Gorge, Tanganyika. Nature 191: 478-479. London.

Leakey, M.D.
1981 Tracks and Tools. Philosophical Transactions of the Royal Society of London, B 292: 95-102.

Leakey, M.D. and R.L. Hay
1979 Pliocene footprints in the Laetoli Beds at Laetolil, N. Tanzania. Nature 278: 317-323. London.

Leakey, M.D., R.L. Hay, G.H. Curtis, R.E. Drake, M.K. Jackes and T.D. White
1976 Fossil hominids from the Laetolil Beds, Tanzania. Nature 262: 460-466. London.

Lee, J.S.
1939 The Geology of China. London: Murby.

Li, Y.
1981 On the subdivisions and evolution of the Quaternary mammalian faunas of South China. Vertebrata PalAsiatica 19(1): 67-75 (in Chinese, English summary 75-76).

Liu, T.S. and C.Y. Chang
1962 The Loess of China. Acta Geologica Sinica 42. (in Chinese).

Liu, T.S., M.H. Liu, T.J. Wu and C.H. Cheng
1964 On the stratigraphic division of the Chinese Quaternary. *In*: Problems of the Geology of the Quaternary, Complied by Institute of Geology, Academia Sinica. pp. 45-64 (in Chinese).

Ma, X., F. Qian, P. Li and S. Ju
1978 Paleomagnetic dating of Lantian Man. Vertebrata PalAsiatica 16(4): 238-243 (in Chinese).

McFadden, P.L., A. Brock and T.C. Partridge
1979 Palaeomagnetism and the age of the Makapansgat hominid site. Earth and Planetary Science Letters 44: 373-382.

Movius, H.L.
1948 The Lower Paleolithic cultures of southern and eastern Asia. Transactions of the American Philosophical Society, n.s. 38(4): 329-420.

Oakley, K.P.
1953 Dating fossil human remains. *In*: A.L. Kroeber (ed.), Anthropology Today. pp. 43-56. Chicago: University of Chicago Press.

1966 Frameworks for Dating Early Man. Chicago: Aldine.

Pei, W-c.
1957 The zoogeographical divisions of Quaternary mammalian faunas in China. Vertebrata PalAsiatica 1(1): 9-24.

Penck, A. and E. Brückner
1909 Die Alpen im Eiszeitalter. Leipzig: Tauchnitz.

Ruddiman, W.F. and A. McIntyre
1973 Time-transgressive deglacial retreat of polar water from the North Atlantic. Quaternary Research 3: 117-130.

Ruddiman, W.F. and A. McIntyre
1976 Northeast Atlantic paleoclimatic changes over the past 600,000 years. *In*: R.M. Cline and R.D. Hays (eds.), Investigation of Late Quaternary Paleoceanography and Paleoclimatology. Geological Society of America Memoir 145: 111-146.

Santa Luca, A.P.
1980 The Ngandong Fossil Hominids: a Comparative Study of a Far Eastern *Homo erectus* Group. Yale University Publications in Anthropology 78.

Sartono, S.
1976 Genesis of the Solo terraces. Modern Quaternary Research in S.E. Asia 2: 1-21.

1979 The stratigraphy of the Sambungmacan site, Central Java. Modern Quaternary Research in S.E. Asia 5: 83-88.

Sartono, S., F. Semah, K.A.S. Astadiredja, M. Sukendarmono and T. Djubiantono
1981 The age of *Homo modjokertensis*. Modern Quaternary Research in S.E. Asia 6: 91-102.

Schaefer, I.
1956 Sur la division du Quaternaire dans l'avantpays des Alpes en Allemagne. IV INQUA Congress Actes, II: 910.

Semah, F., S. Sartono, Y. Ziam and T. Djubiantono
1981 A paleomagnetic study of the Plio-Pleistocene sediments from Sangiran and Simo (Central Java): Initial results. Modern Quaternary Research in S.E. Asia 6: 103110.

Shackleton, N.J. and N.D. Opdyke
1973 Oxygen isotope and paleomagnetic stratigraphy of equatorial Pacific core V28-238: Oxygen isotope temperatures and ice volumes on a 10^5 and 10^6 year scale. Quaternary Research 3: 39-55.

1976 Oxygen isotope and paleomagnetic stratigraphy of Pacific core V28-239, late Pliocene to latest Pleistocene. *In*: R.M. Cline and R.D. Hays (eds.), Investigations of late Quaternary paleoceanography and paleoclimatology. Geological Society of America, Memoir 145: 449-464.

Siesser, W.G. and D.W. Orchiston
1978 Micropaleontological re-assessment of the age of Pithecanthropus mandible C from Sangiran, Indonesia. Modern Quaternary Research in S.E. Asia 4: 25-30.

Sun, D-g., M-l. Chou and X-h. Wu
1981 Brief notes on Quaternary glaciations in China. *In*: V. Sibrava and F.W. Shotton (eds.), Quaternary glaciations in the Northern Hemisphere. Report No.6: 244-262. Prague: Geological Survey for INQUA.

Taieb. M.
1974 Evolution Quaternaire du bassin de l'Awash. Ph.D. dissertation l'Université de Paris VI. 390 pp. (unpublished).

Teilhard de Chardin, P.
1941 Early Man in China. Pekin: Institute de Geó-Bioloie.

Wang, L. and L. Ouyang
1982 Subdivision of Ailuropoda-Stegodon fauna by applying cluster analysis. Vertebrata PalAsiatica 20(3): 257-263 (in Chinese, English summary p. 263).

Wu, X.
1981 A well-preserved cranium of an archaic type of *Homo sapiens* from Dali, China. Scientia Sinica 24(5): 530-641.

Xu, Q. and L. Ouyang
1982 Climatic change during Peking Man's time. Acta Anthropologica Sinica 1(1): 80-88 (in Chinese, English summary 89-90).

Zagwijn, W.H.
1975a Chronostratigrafie en biostratigrafie: Indeling van het Kwartair op grond van veranderingen in vegetatie en klimaat. *In* W.H. Zagwijn and C.J. van Staalduinen (eds.), Toelichting bij geologische overzichtskaarten van Nederland. pp. 109=114. Haarlem: Rijks Geologische Dienst.

1975b Variations in climate as shown by pollen analysis, especially in the Lower Pleistocene of Europe. *In*: A.E. Wright and F. Mosley (eds.), Ice Ages: ancient and modern. pp. 137-152. Liverpool: Steel House Press.

Zagwijn, W.H. and C.J. van Staalduinen
1975 Toelichting bij geologische overzichtskaarten van Nederland. Haarlem: Rijks Geologische Dienst.

Hominid Evolution in Africa

PHILLIP V. TOBIAS
Medical School, University of the Witwatersrand
JOHANNESBURG 2193, R.S.A.

Abstract: Three strategies characterize the study of man's evolution at various depths in time. First, the phase of hominid emergence (between 7 and 4.5 mya [million years ago]) is illuminated by (a) the paleo-anatomy of the available fossils; (b) comparative morphology (including chromosomal morphology, and (c) comparative molecular biological study of living hominids and non-hominids. Secondly, the analysis of the evolution of the established hominids (from 4.0 million to 1.0 mya) is largely a paleo-anatomical and archaeological undertaking, to which molecular biological and genetical approaches contribute but little. Thirdly, the phase of modern human evolution (from 1.0 mya until today) rests heavily on anatomical and molecular biological approaches, together with those of archaeology, social anthropology, ethnology, linguistics, ecology and ethology.

This paper concentrates on hominid evolution in Africa in the middle period (4.0-1.0 mya). A rich stockpile of hominid fossils dating from this period is available in Africa. From Taung in the South — with its *Australopithecus africanus* child — to Hadar with its 'Lucy' in the north, the African continent has yielded early hominid fossils of no fewer than 500 individuals of one kind or another, and of varying degrees of incompleteness. These fossil finds permit us to make inferences about the history and role of *Australopithecus* and its diverse species; about the emergence, at a dramatic evolutionary radiation or punctuation, of the genus *Homo* between 2.5 and 2.0 mya; and about the gradual phyletic change of early *Homo* through three time-sequent species to modern man. In short, a fairly clear picture of the tempo and mode of hominid evolution is emerging: the picture conforms with neither the Eldredge-Gould model of punctuated equilibrium alone, nor the 'opposite' concept designated phyletic gradualism alone. Instead it partakes of aspects of both models: the pattern of change is somewhat as Charles Darwin delineated in the fourth edition of *The Origin of Species* (1866). Thus, there are phases of phyletic gradualism, one of which shows marked phyletic change of the genus *Homo* over the past two million years. There is also one striking mode or punctuation between 2.5 and 2.0 mya. A third pattern of phylogenetic change is suggested in the later stages of modern human evolution, at least from *Homo erectus* onwards, namely reticulate evolution. Thus, a single evolutionary model does not fit the established facts of hominid evolution: the pattern of phylogeny itself varies at different times and under varying circumstances.

Evidence is adduced that a form of articulate speech had emerged already in *Homo habilis* by at least 1.8 mya.

Résumé: L'étude de l'évolution de l'homme à travers les âges se divise en trois étapes. La première, celle de l'apparition de l'hominide entre 7.0 et 4.5 millions d'années, est éclairée par (a) l'étude paléo-anatomique des fossiles connus, (b) la morphologie comparative (y compris la morphologie chromosomique), et (c) l'étude biologique moléculaire comparative des hominides et non-hominides actueles. En second lieu, l'analyse de l'évolution du groupe hominide établi (de 4.0 à 1.0 million d'années) faite surtout par les études paléo-anatomiques et archéologiques, la biologie moléculaire ainsi que l'évidence génétique, ne contribuent que très peu d'information à cette période. Troisièment, l'étape de l'évolution humaine moderne (de 1.0 million d'années jusqu'à présent) dépend en majeure partie des approches génétiques et anatomiques ainsi que de l'archéologie, l'anthropologie sociale, l'ethnologie, la linguistique, et de l'éthologie. Cette discussion porte en majeure partie sur l'évolution de l'hominide en Afrique durant la période intermédiaire, c'est-à-dire de 4.0 à 1.0 million d'années. Une impressionnante collection de fossiles hominiens datant de cette période nous provient d'Afrique. De Taung au sud qui nous a livré l'enfant *Australopithecus africanus* à Hadar plus au nord où l'on retrouve 'Lucy', le continent africain nous révèle la présence fossilisée de non moins de 500 hominides plus ou moins complets et de type varié. Ces trouvailles nous permettent de tirer certaines conclusions sur l'histoire et le rôle tenu par l'Australopithèque et ses diverses espèces; sur l'apparition, soit par rayonnement évolutionnaire accéléré ou par ponctuation, du genre *Homo* entre 2.5 et 2.0 millions d'années; ainsi que sur le changement phylétique de l'Homme primitif (*Homo*) en l'Homme moderne à travers ses 3 espèces consécutives. Bref, une image assez précise du rythme ainsi que du mode évolutionnaire hominien prend forme. Cette image ne s'aligne ni sur le modèle Eldredge-Gould d'équilibre ponctué ni sur le concept de progression phylétique qui lui est opposé mais tient plutôt d'un amalgame des deux modèles: le changement s'accomplit selon des principes semblables à ceux qu'a proposé Charles Darwin dans sa quatrième édition de *L'Origine des Espèces* (1866). L'on perçoit donc des phases de progression phylétique, l'une d'elles démontrant un changement phylétique marqué du genre *Homo* au cours des deux derniers millions d'années. Une ponctuation ou mode frappant est aussi perceptible entre 2.5 et 2.0 millions d'années. Un troisième type de changement phylogénétique fait son apparition au cours des périodes les plus récentes de l'évolution humaine moderne, du moins à partir de la période d'*Homo erectus*, soit l'évolution rétiforme. Un seul modèle évolutionnaire ne couvre donc pas toutes les données de l'évolution de l'hominide: le schéma phylogénique varie lui-même à différentes périodes et selon les circonstances.

L'évidence suggère qu'une forme de langage articulé était déjà présente chez *Homo habilis* il y a 1.8 million d'années.

Key Words: **Hominid, evolution, Africa, Australopithecines, speech.**

STRATEGIES IN THE STUDY OF MAN'S BIOLOGICAL EVOLUTION

When we speak of hominid evolution, in general, we refer to a holistic concept of development. It embraces biological, ecological, behavioural, and cultural evolution. These modalities are interrelated and it may be difficult to draw sharp dividing lines between any two of them. Nevertheless, in this analysis, I shall for the most part confine my attention to biological evolution.

Strategy One: The Phase of Hominid Emergence

The emergence of the Hominidae (the zoological family of man) has been illuminated by two major sets of data, the fossil evidence and the molecular biological evidence, to which should be added the testimony of a third set, the chromosomes, as studied today by refined banding and cellular hybridization techniques. At one time, the fossils, enlivened by the insights furnished by the comparative anatomy of related living forms, provided the exclusive basis of statements about hominid biological evolution. Within the last two decades, other groups of scholars, the molecular biologists, have brought a new light to focus on the problem of hominid origins. The study of molecular systematics and evolution is based on immunological, protein sequencing, and DNA hybridization data. The application of these data to the problem of hominid origins was effected by the upholders of these methods, generally with but little regard to comparative anatomical or paleontological data, at least until recently.

By 1974, when a Wenner-Gren Foundation symposium on "The Role of Natural Selection in Human Evolution" was held in Burg Wartenstein, Austria (Salzano, 1975), a controversy could be recognized which, in over-simplified terms, could be summarized as 'fossils against molecules':

> '....the bases of this controversy are (a) the widely held belief that paleontological evidence points to the early emergence of the Hominidae (15 to 20 mya) and (b) an interpretation of the molecular evidence as pointing to a late separation of Hominidae from Pongidae (either 4 to 8 or 5 to 10 mya). For a time this disagreement threatened to deteriorate into a classical conflict of the 19th century variety, the two standpoints being epitomized by such assertions as 'Fossils are more important, because they provide the hard facts of evolution' and 'Molecules are more important, because they are close to the genes — and it is genotypes that evolve.' (Tobias 1975a: 90)

I pleaded then for the two concepts and the two lines of data to be employed jointly in a synthetic approach to the study of human evolution, and I expressed the view that "The fossil data bearing on hominid evolution are reconcilable with the evidence of close molecular similarities between living pongids and *Homo sapiens*" (op. cit.: 114).

Since that time, molecular biologists have looked more closely at their concepts, presuppositions and data, while paleontologists have examined more critically their fossils. As a result, the hoped-for synthesis between the paleontological and molecular approaches and conclusions has been in large measure achieved. The synthesis was presaged in the volume edited by Salzano (1975), heralded in the symposium entitled 'Miocene Hominoids and New Interpretations of Ape and Human Ancestry' organised by R.L. Ciochon and R.S. Corruccini (1982) at the VIIIth Congress of the International Primatological Society in Italy in July 1980, and consummated at a meeting of a dozen scholars from six countries held at the Pontifical Academy of Sciences in the Vatican in May 1982, on 'Recent Advances in our Knowledge of Primate (including Human) Evolution' (and in which the author was privileged to be a participant).

It may be accepted today that the major strategy involved in studies on the emergence of the hominids from non-hominids, and in the divergence of hominids from pongids, is based on evidence from three major sources — the fossil and archaeological records, comparative morphology (including chromosomal morphology) and comparative molecular biology.

Strategy Two: The Phase of the Evolution of Established Hominids

Once the hominids had become separated from the pongids, the study of their subsequent biological evolution as established hominids — from about 4.0 mya until relatively recent times — is largely a paleo-anatomical undertaking. Comparative molecular data play very little if any part in untangling the skeinwork of evolutionary patterns *within* the Hominidae. It is within this middle period (about 4.0 to 1.0 mya — or, before the present) that archaeological and ethological evidence plays an ever-increasing role in the unravelling of the patterns of human evolution in the general sense. The biological changes within this period are, however, largely predicated upon the fine study of the paleo-anatomy of the fossils: the study of such changes is enriched by the parallel testimony of material culture and the broad inferences which may be drawn from it, on such aspects as group size, distribution, food-habits, technical and rational intelligence, speaking ability, the world of ideas of the evolving hominids, as the Pliocene gives way to the Pleistocene and thereafter.

Strategy Three: The Phase of Modern Human Evolution

Finally, the history of the emergence of biologically modern man and of his global varieties rests heavily on anatomical or physical anthropological evidence, and on the evidence of genetical variations in modern human populations. The anatomical study in this third phase rests on close comparisons among living human communities and on the well-dated and increasingly numerous fossil remains; whilst the human population geneticist is able to use the invaluable tool of gene frequency studies as a kind of excavator of the past, as it throws light on the genetic interrelations of human populations. As in the second phase, the role of the archaeologist in casting light on the emergence of modern patterns of behaviour is immeasurable, while the more recent phases are illuminated by the insights of social anthropology, ethology, linguistics and ethnology.

In sum, we may recognise three phases of hominid biological evolution, to each of which a different armamentarium of strategic biological approaches provides the key:

The phase of hominid emergence

(before 4.0 mya)
-paleo-anatomy of the fossils
-comparative morphology (including chromosomal morphology)
-molecular biological study of living hominids and non-hominids

The phase of the evolution of established hominids

(4.0-1.0 mya)
-paleo-anatomy of the fossils
-archaeological approach

The phase of modern human evolution

(1.0 mya–today)
-anatomical study of the fossils and of modern human populations
-molecular biological study of modern human populations
-approaches of archaeology, social anthropology, ethnology, linguistics, and ethology

THE PHASE OF HOMINID EMERGENCE

A prime objective of the meeting held in the Pontifical Academy of Sciences in May 1982 was to reconcile the inferences from the paleontological with those from the molecular biological evidence. It would be worthwhile here to review some of the main conclusions of that meeting, as set out in an agreed statement shortly to be published and to which the author was a party:

The first point was the unanimous reiteration by the group that the process of evolution of living things is the accepted basis of modern biology.

> More specifically, in the field of primate studies, evolution is a highly confirmed and widely supported hypothesis, and in the discipline of human biology, the evolutionary hypothesis occupies a central and unavoidable place.
>
> The working group reviewed the fossil, morphological and biochemical evidence for the temporal and genetic relationships among fossil and living primates and appraised the early hominid fossil record. A major issue during the past two decades has been this question: whether the latest common ancestor, from which various living apes and man descended, lived as much as 20 mya (the Early Divergence Hypothesis), or whether the ape-hominid split occurred as recently as 5-7 mya (the Late Divergence Hypothesis). The principal evidence for early divergence has been the fossil record of the hominoid *Ramapithecus* which is dated from 7-16 million years, and which has until recently been considered by some to be hominid (that is, a member of the Hominidae and so on the human line). The strongest evidence for late divergence is a mass of biochemical data showing about 99 per cent identity between the DNA and proteins of chimpanzee, gorilla and man which — from inferred rates of DNA and protein change — implies that these lineages separated from one another only 5-7 mya.

The need for such a review has been stated clearly by Ciochon and Corruccini (1982) in a report on an independent meeting on a similar theme:

> The last five years have witnessed a reconceptualization of the affinities of the Miocene hominids vis à vis the modern apes and man.....this reconceptualization has been brought about by at least five independent factors. These can be summarized as:
>
> 1. New fossil discoveries which have increased doubt about the hominid affinities of *Ramapithecus*.
>
> 2. The discovery of many additional new Miocene hominoid specimens, especially *Sivapithecus*, including several partial skulls from various geographical regions in the Old World, particularly in China...
>
> 3. Recent reinterpretations regarding the postcranial data in Miocene material from Potwar and Rudabanya as opposed to the more primitive remains known from lower Miocene deposits in Africa.
>
> 4. The increasing acceptance or influence of biochemical data for understanding the timing and relationships of hominoid cladogenesis.
>
> 5. The incredible discovery of a large sample of 3-4 million-year-old hominids from Eastern Africa that have unexpectedly chimpanzee-like characteristics. (Ciochon and Corruccini 1982: 149)

The crucial position of *Ramapithecus* — asserted so strongly by some to be hominid (Lewis 1934, Simons 1961, 1964, 1968, Simons and Pilbeam 1965, Pilbeam 1966, 1968, Conroy and Pilbeam 1975,) and whose hominid status has been doubted or denied by others (Genet-Varcin 1969, Wolpoff 1971, Eckhardt 1972, 1973, Robinson 1972, Vogel 1975) — is pivotal to the argument about Early and Late Divergences. Most of the participants in this controversy were referring to the genus *Ramapithecus* as a whole, including both its Indian and its African species. On the other hand, it is interesting to note that von Koenigswald (1972, 1973) adjudged the Indian and African forms to be different. The type species *Ramapithecus punjabicus* he regarded as a hominid, but he considered the African species *R. (Kenyapithecus) wickeri* to be a pongid species, and not a member of *Ramapithecus* at all.

Both the Ciochon-Corruccini meeting and the Vatican working group agreed it is no longer tenable to consider *Ramapithecus* as being hominid. It may not even be on the hominid line and the Vatican group concluded that it is more likely that *Ramapithecus* is on the line leading to the orangutan.

The consensus reached at the Vatican meeting — which brought together paleontologists, molecular biologists, a cytogeneticist and general paleo-anthropologists — may be summarised in the following extracts from the Agreed Statement:

> The African fossil record gives evidence of arboreal primates that lived between 35 and 25 mya in the Egyptian Fayum. One or more of these species appear to have been ancestral to the Old World monkeys, apes and man. Hominoid genera (including *Ramapithecus, Sivapithecus* and others) lived in Africa, Asia and Europe between 16 and 7 mya.
>
> Comparative morphology (including that of the chromosomes) indicates a close relationship between *Homo sapiens* and the African apes (chimpanzee and gorilla). This closeness has been confirmed by numerous molecular biological studies which have compared DNA and the proteins of man with those of other living primates. Most changes in DNA base pairs, the hereditary material, are effectively neutral and do not appear to influence evolutionary fitness. Therefore, the inferred rate of change between lineages can be used to identify, and to estimate dates for, the main branchings of the primate family tree. On the basis of molecular and all other available evidence, the lineages leading to man, chimpanzee and gorilla seem to have diverged from their common ancestor as recently as 5 to 7 mya, whereas the orangutan diverged 10 to 16 million years ago. These divergence times are consistent with the known fossil record.

In another recent attempt to arrive at the timing of the hominid-pongid divergence, J.E. Cronin employed a synthetic approach based on various immunological, protein sequencing, DNA hybridization, and chromosome morphological data. On this basis he arrived at an approximate date of 4.5 mya, though this might possibly have been as high as 5.5 mya (cited by Ciochon and Corruccini 1982: 156).

Hence, we have two recent estimates which overlap in part: that emanating from the meeting in the Pontifical Academy of Sciences, namely, 5-7 mya and that of Cronin, namely 4.5-5.5 mya. Five mya would seem to be a reasonable estimate for the time of emergence of the hominids, that is, close to the Miocene-Pliocene boundary on most current views (Howell 1978).

The fossil record has in recent years yielded a number of specimens close to the crucial time period (Table 1).

Mary Leakey's group of fossils from Laetoli, and those from Hadar in Ethiopia described by Johanson and White (1979), have been identified by their describers as a new, more primitive species of *Australopithecus*, namely *A. afarensis*. Tobias (1980a) and Day, M.D. Leakey and Olson (1980) have questioned the correctness of the procedures followed in the creation of the proposed new species and the former worker has queried whether these East African specimens are demonstrably distinct from the previously defined oldest species of *Australopithecus*, namely *A. africanus* as known from South Africa. Several studies have drawn attention to the chimpanzee-like features of these early East African australopithecines (though it should not be forgotten that chimpanzee resemblances of *Australopithecus africanus* have been noted since the earliest days of the Taung discovery!). In the present context, however, the markedly chimpanzee-like features that are said to characterize the Hadar and Laetoli fossils have led paleontologists to feel that the oldest of those fossils, dated to about 3.5-3.7 mya, could not long have diverged from the

TABLE 1

Some Early East African Hominoid Fossils

BP Myr.	SPECIMEN	AFFINITY	LOCALITY
4.0	5 cranial fragments and part of femur	Hominid	*Middle Awash* Valley, Ethiopia (1981)
4.0 or less	Temporal bone	Hominid	*Chemeron*, Kenya (1965)
4.0-5.0	Distal humeral fragment	Hominid (?*Australopithecus*)	*Kanapoi*, Kenya (1965)
5.0-6.0	Fragment of maxilla with one molar tooth	?Hominid (*Australopithecus*)	*Lothagam*, Kenya (1967)
ca. 6.5	Lower molar tooth	?Hominid	*Lukeino*, Kenya (1973)
ca. 8.0	Mandible with 5 molar teeth	Hominoid	*Samburu Hills*, Kenya (1982)
ca. 10.0 (>9.6-9.8)	Upper molar tooth	Hominoid	*Ngorora*, Kenya (1968)

latest common ancestor of the pongids and hominids. This interpretation is consistent with the inferences from molecular data that the divergence is likely to have occurred between 4.5 and 7.0 mya.

Does our fossil record take us any closer to the critical time of divergence?

A molar tooth from Lukeino, east of the Tugen Hills in Central Kenya, is bracketed between formations dated to ca 5.4 and 7.0 mya and is most likely to have been about 6.5 mya. This specimen would appear to lie in the crucial time zone: it is a hominoid lower molar that has distinct hominid resemblances (Howell 1978).

A lower jaw fragment, containing one molar tooth, stems from Lothagam Hill southwest of Lake Turkana: it is dated to about 5 to 6 mya. Like the Lukeino tooth, the specimen is too incomplete to enable one to be sure of its affinities, but it has been commonly regarded as a hominid mandible (Patterson, et al. 1970; Tobias 1975a; Howell 1978).

Between 5 and 4 mya, we have until recently had only two claimants for hominid status. One is a distal humeral fragment from Kanapoi in the southwest part of Turkana District, northern Kenya (Patterson and Howells 1967). The other — those dating may, in fact, be somewhat younger (Tobias 1975a) — is a well-preserved temporal bone from the Chemeron Beds in the basin of Lake Baringo, Central Kenya (Martyn and Tobias 1967).

These remains of Lukeino, Lothagam and Kanapoi are so incomplete and even nondescript that they throw little light on the nature of the hominid represented (if, indeed, it is in each case a hominid). One or more of them might have belonged to the earliest hominids, or to the latest common ancestral population of pongids and hominids.

In the Samburu Hills of Northern Kenya, a maxilla with five molar teeth is reported to have been found on 27th August 1982 by a Japanese team from Osaka University led by Dr. Hidema Ishida: the discovery was announced at a press conference in Nairobi on 31st August 1982 by Dr. Ishida and Richard Leakey. The deposit has been tentatively dated to about 8 mya. More details are awaited.

Another announcement of East African discoveries was made the same year. On 10th June 1982, J. Desmond Clark and T.D. White made known the discovery in autumn 1981 of five cranial fragments and part of a femur dated to 4.0 mya, from the Middle Awash River valley in the Afar Triangle of north-central Ethiopia. These bones would seem to be older than any previously discovered at Hadar and they are even closer to the crucial time zone of pongid-hominid divergence. The femur is described as indicating bipedalism and the cranial fragments are estimated to have been part of a calvaria of capacity ca 400 cc., close to the lowest value for a Transvaal *A. africanus* (428 cc. for both Sts 60 and Sts 71 — Holloway 1975). These Middle Awash specimens come from an area in which the sediments go back to at least 6.0 mya, according to Clark (1982, pers. comm.). The latest expedition might well have sampled part of the earliest population of declared hominids (Clark and White 1982).

So the net of paleontological discovery is closing in on the critical time-zone indicated by the biomolecular researches. There is now little room for doubt that the combined approach of paleontology, comparative morphology and molecular biology has converged on the very moment of hominid emergence.

THE EVOLUTION OF ESTABLISHED AFRICAN HOMINIDS

(4.0 to 1.0 mya)

In the 25 years that have elapsed since the University of Alberta celebrated its golden jubilee, the study of human paleontology has made enormous strides in Africa. In 1957, only seven sites in Africa had yielded fossils of what are today accepted as early hominids. Five of these were in the Union of South Africa and they included Taung, the site of the earliest discovery of an australopithecine. The other South African sites were Sterkfontein (1936 onwards), Kromdraai (1938 onwards), Makapansgat (1947 onwards) and Swartkrans (from 1948). The two remaining sites were in Tanganyika of those days, namely Olduvai and Garusi (now known as Laetoli). The few fragments from these two East African localities represented at most five individuals, while the five South African sites represented a good sample of not fewer than 121 individuals and possibly as many as 157 individuals. To take the middle value, remains of some 144 early fossil hominid individuals were available from seven African sites a quarter of a century ago.

By today, instead of seven we have 14 and possibly several more African sites that have yielded early hominids (Table 2).

TABLE 2

African Sites of Early Hominid Discoveries

1924		1957		1982	
1 Site		**7 Sites**		**14-18 Sites**	
South Africa	1	South Africa	5	South Africa	5
		Tanzania	2	Tanzania	3
				Kenya	3-7
				Ethiopia	2
				Chad	1

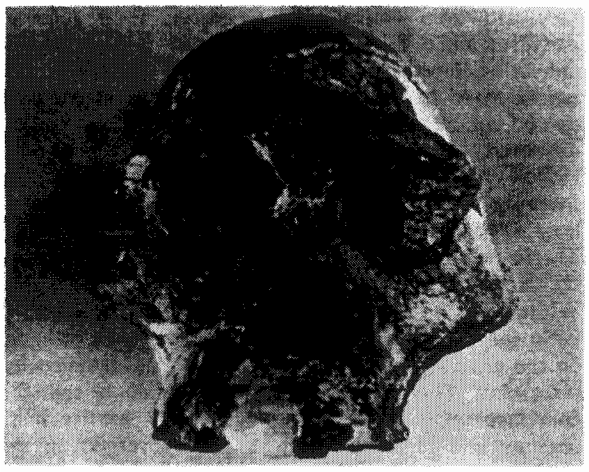


Figure 1. Sterkfontein hominid 5, the most complete cranium of *Australopithecus africanus transvaalensis*, found by Dr. Robert Broom and Dr. John T. Robinson, on 18th April 1947. The stratum from which this *in situ* specimen emanated has now been designated Member 4 of the Sterkfontein Formation. Faunistically it has been dated to between 2.5 and 3.0 million years B.P.

Figure 2. The back of the cranium of *Australopithecus africanus transvaalensis* (MLD 1) from Makapansgat, Northern Transvaal. This specimen comprises a large part of the occipital bone and major portions of the two parietal bones, with an interesting pattern of sutures or joint-lines between them. It was the first ape-man specimen to be found at Makapansgat and was discovered by James Kitching in September 1947.

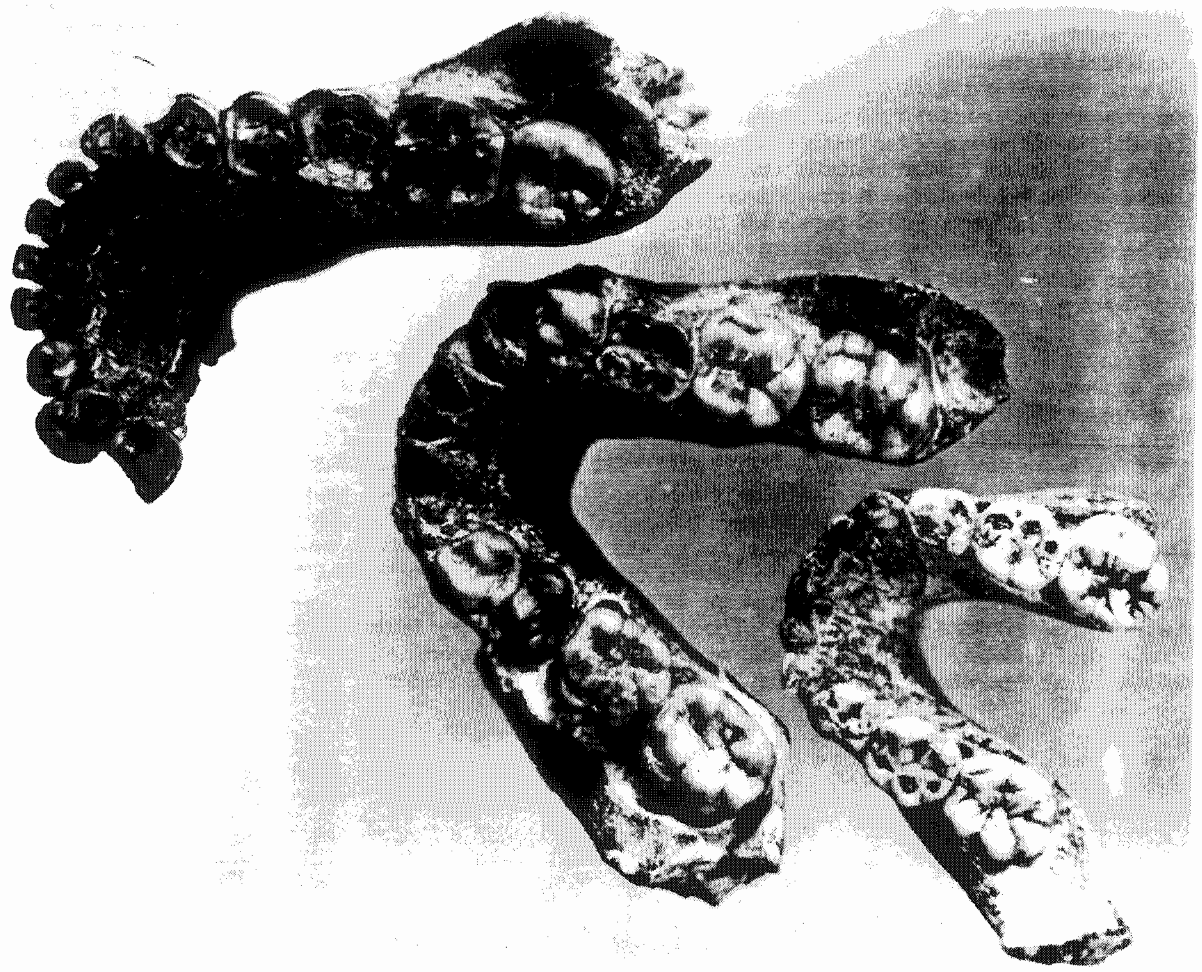


Figure 3. Three South African australopithecine jaws: from right to left, the child jaw of Taung of about 5-6 years of age by modern standards; the juvenile mandible of Makapansgat of about 11-12 years old; and an adult jaw from Makapansgat in which not only had the right wisdom tooth erupted but it had been in use sufficiently long to produce some attrition of the surface of the crown.

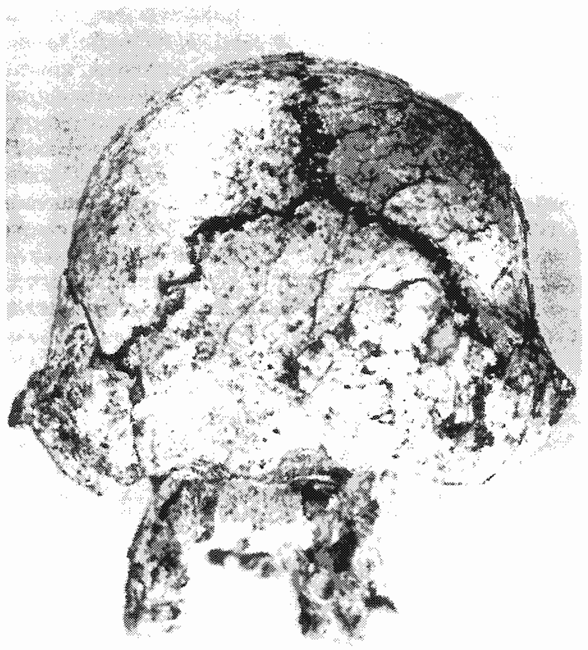


Figure 4. Superbly preserved posterior two-thirds of cranium MLD 37/38 of *Australopithecus africanus transvaalensis* from Makapansgat 320 kilometres north of Johannesburg. The cranium belonged to an adolescent or sub-adult individual with incompletely erupted wisdom teeth and widely-open sutures between the calvarial bones at the time of death.

The number of South African sites has remained five, but six to nine new East African sites and one Saharan place-name have been added to the catalogues of African fossil man discovery sites. The term 'site' does scant justice to some of them, for several sites in Tanzania, Kenya and Ethiopia cover hundreds of square kilometres each. The new site in Tanzania is Peninj on Lake Natron; six new sites in Kenya are the Chemeron Beds, Chesowanja and Lukeino near Lake Baringo, Koobi Fora, Kanapoi and Lothagam near Lake Turkana (formerly Lake Rudolph). There are two new sites in Ethiopia, namely the Omo Valley in the south and the Afar Depression (Hadar) in the north-east; and Yayo (Koro Toro) in the Chad Republic.

The number of individuals represented from the sites of South and East Africa has more than trebled. Instead of a minimum of 121 individuals, as in 1957, we have at our disposal an estimated minimum of 405 early fossil hominids and a possible maximum of 617 individuals, with a middle value of some 511 individuals (Table 3).

One of the extra sites in Kenya referred to in Table 1 is Ngorora in the Tugen Hills west of Lake Baringo. A single hominoid upper molar tooth has come from this site and some have thought it to have hominid affinities: its age is close to 10.0 mya, but it is not a convincing claimant to hominid status. The possible Kenyan sites include Lothagam and Kanapoi southwest of Lake Turkana, but the mandibular and humeral fragments from here might or might not have belonged to hominids. The same is true of the central Kenyan specimen of Lukeino.

To a human population biologist, for whom the sample size is often a critical consideration, 511 individuals is only a modest sample, especially when one considers that these 511 indivudals spanned no less than three million years. If our fossils were evenly spaced in time — which of course they are not — we should have one individual for every 5871 years!

Moreover, the stockpile of early hominid fossils, on most classificatory systems used today, falls into two genera, *Australopithecus* and *Homo*, and into different species, most commonly reckoned as four to six in number, over the time period under consideration. Each species itself was dispersed in time and space, allowing of geographical and temporal variability. Demographically, each deme comprised two sexes and individuals of different ages. When our data are broken down according to all of these categories, the sizes of the sub-sets of fossil individuals are still woefully small.

Notwithstanding, accidents of preservation and the operation of taphonomic agencies have resulted in much of the data being grouped into several fairly large sub-sets, such as the remarkable South African type collection of *A. africanus transvaalensis* from Sterkfontein and Makapansgat (comprising over 80 individuals according to my most recent estimates) and of *A. robustus crassidens* from Swartkrans (which at the latest tally numbers close on 90 individuals, according to the middle value of the range of estimates). These estimates are, of course, only provisional. Detailed demographic estimates have been made for the South African sites (Mann 1968, 1975; Tobias 1968,1974a) and for Olduvai (Tobias 1982) and some 245 individuals (middle value) have been identified from these site-samples. However, we still await detailed demographic analyses of the samples from several of the richest East African sites, namely, Laetoli, Koobi Fora, Omo and Hadar. The figure of 260 individuals for the East African site-samples (excluding Olduvai) is therefore only a crude estimate and it is as far as the published accounts permit us to go at present.

Despite the shortcomings of the fossil hominid data, the almost explosive increase in the number of specimens in the past quarter of a century has given us a much clearer picture of the morphological nature of the hominids and of the pattern of hominid evolution.

TABLE 3

25 Years of African Early Hominid Discoveries

1957	1982
From **7** sites	From **15** sites
121-157 individuals represented	**405-617** individuals represented
Mid-value **144** individuals	Mid-value **511** individuals

The first of the two hominid genera recognized in the fossil record is *Australopithecus*. The earliest well-attested members are dated to about 3.7 million years (myr) before the present, while the latest survived up to about 1.0 mya. The other genus, *Homo*, the same to which modern man belongs, seems to have made its appearance late in the Pliocene epoch, round about 2.3 mya and, of course, the genus is extant today through its sole surviving species, *H. sapiens*. Thus, the known time span of each of the two genera is between two and three million years, though it is quite possible that *Australopithecus* appeared appreciably earlier than the time of the oldest well-identified and well-dated specimens presently available, that is, earlier than the date of ca 3.7 mya, which is the approximate age of Mary Leakey's ancient hominids and footprints at Laetoli in northern Tanzania.

Some late-surviving robust australopithecines were synchronic and often-times sympatric with the earliest defined species of *Homo*. These were the australopithecines from Swartkrans, Transvaal, generally regarded as representing a distinct subspecies, *Australopithecus robustus crassidens* (though considered by Howell 1978, as members of a distinct species, *A. crassidens*), and the excessively large-toothed hyper-robust australopithecines of East Africa, known usually as a separate species, *A. boisei*.

If we disregard these late-surviving robust australopithecines, we have just under four million years from the earliest known *Australopithecus africanus* (called by some *A. afarensis*) to modern *H. sapiens*. The earliest gracile australopithecines possessed already a number of clearly hominid features, such as the hominid dental pattern and indications of uprightness and bipedalism. These features are sufficient for us to accept their owners as members of the family Hominidae, but they are clearly not at the very base of the hominid radiation.

We have seen that it would not be unreasonable to set the base of the hominid radiation about 1 myr earlier than the fossils of Laetoli and the Middle Awash, say, about 5 myr. If we accept this, purely for purposes of the present analysis, we have a span of 5 mya in which an ape-like ancestor to *Australopithecus* became converted to modern man. At an average generation length of about 15 years, we would have a third of a million generations in which all of the morphological hominid traits became established.

Uprightness seems to have come first and to have been established in <100,000 generations, though its perfecting required more than another 100,000

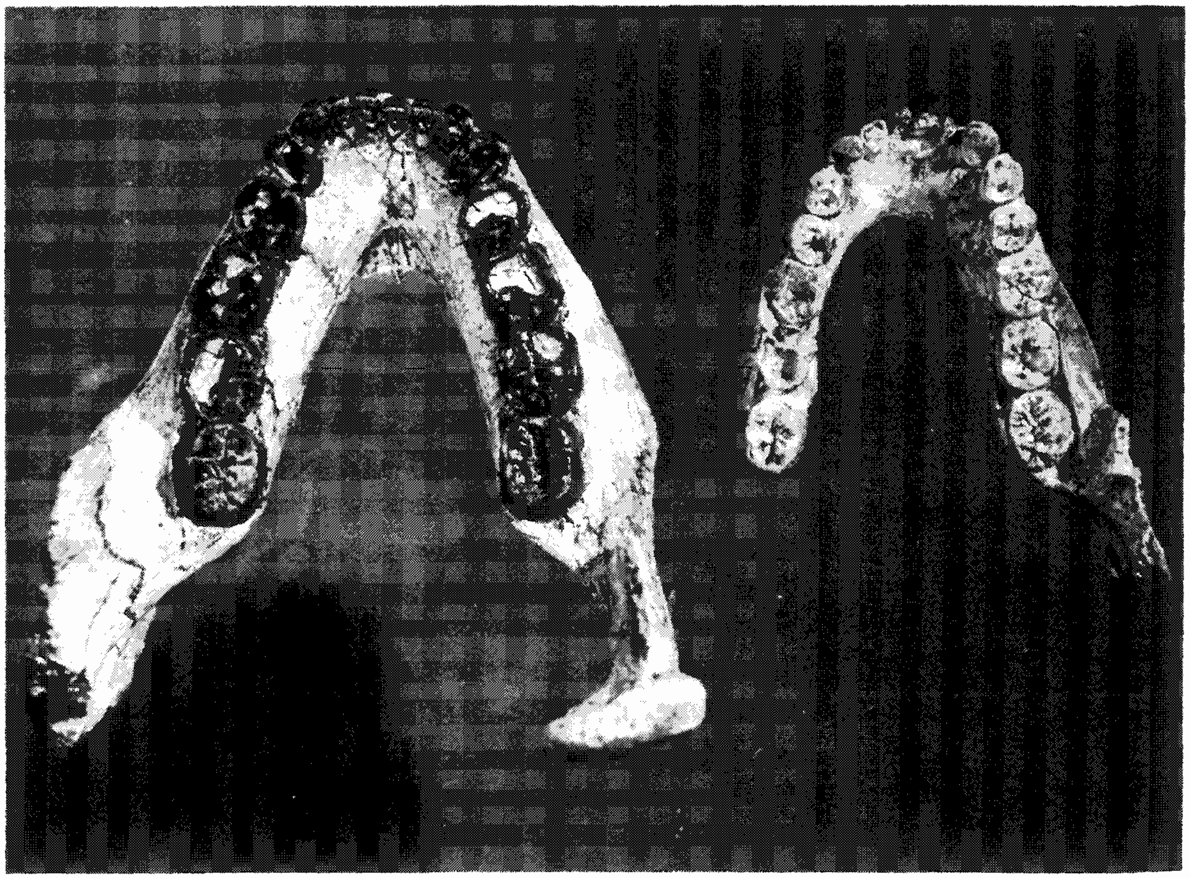


Figure 5. Contrasts in lower jaws of early hominids; on the left, the massive jaw of a late-surviving member of *Australopithecus boisei* from Peninj near Lake Natron in northern Tanzania, a little more than 1 million years B.P.; on the right, the delicately constructed jaw of Olduvai hominid 13, which is about 1.6 million years old and has been identified as the mandible of a female member of the early *Homo* species, *H. habilis*. In *A. boisei*, the small front teeth (incisors and canines) contrast sharply with the monstrously enlarged cheek-teeth (premolars and molars).

generations for fulfilment. The changes in the teeth, also, occurred basically in <100,000 generations before a recognizable hominid pattern emerged, but required >300,000 generations to reach a modern human pattern. Cerebral enlargement was not strikingly manifest for the first 100,000 generations of the period under review, at least in absolute terms, as compared with the brain-size of the extant anthropoid apes. It is possible, however, that, if these earliest hominids were smaller than the living great apes, their possession of modern ape-sized brains would have connoted some early tendency towards relative enlargement of brain-size. We have, however, no real indications of such an early trend towards disproportionate encephalization. The first firm evidence of marked brain enlargement, absolute and relative, shows that the strongly positively allometric encephalizing tendency started late, at the stage of *Homo habilis*, and for the most part filled the time-span from 2.3 to 0.1 mya, that is, a period of about 2.2 million years or just under 150,000 generations.

Hence, as far as the evidence permits us to draw inferences, it seems likely that not only was marked positively allometric enlargement of the cerebrum one of the latest hominizing trends to begin, but the brain attained modern human proportions in the smallest number of generations, compared with the other hominizing trends for which data are available.

Such rapidity of evolutionary change of the brain has been addressed elsewhere and an explanation has been suggested (Tobias 1981a, 1981b).

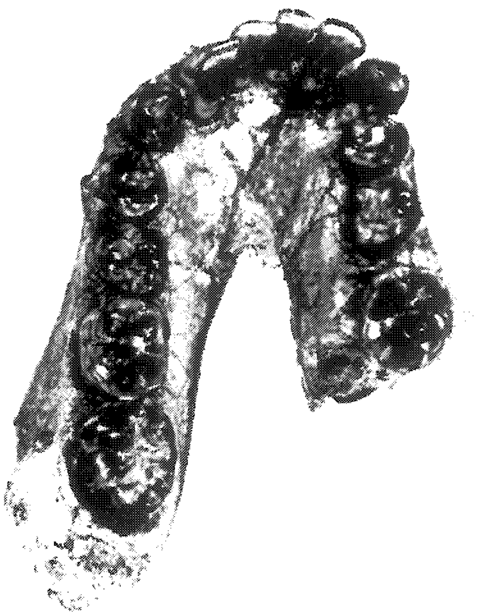
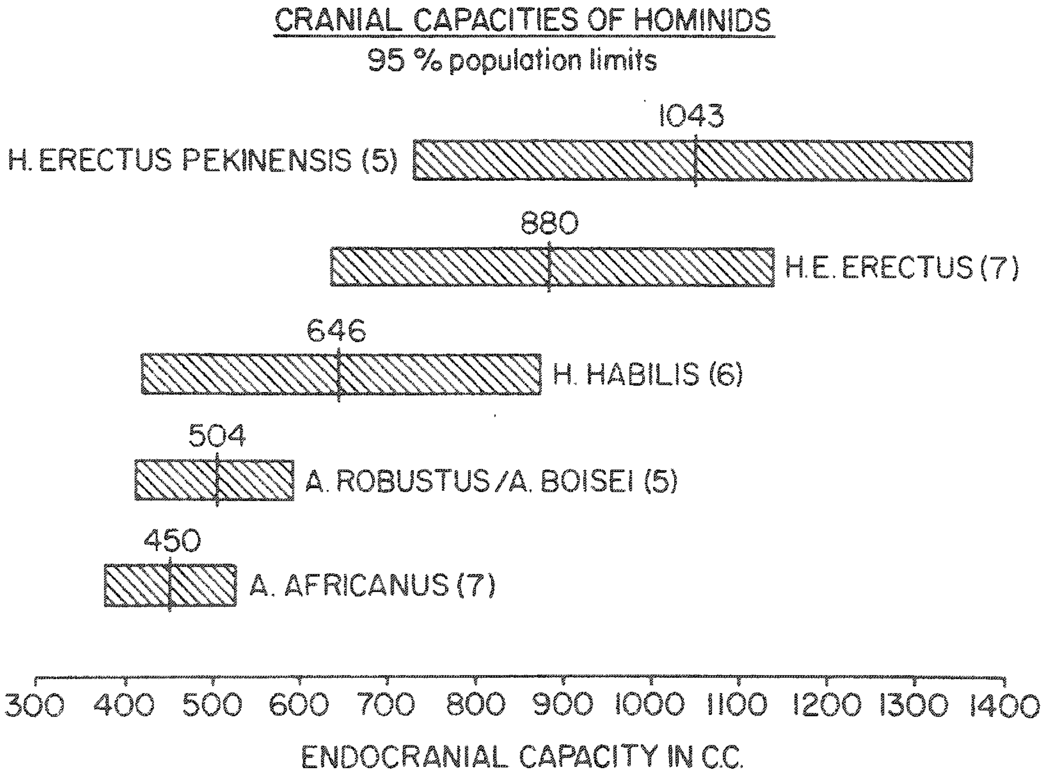


Figure 6. Mandible of the type specimen of *Homo habilis*, recognised as the jaw of a distinct species by L.S.B. Leakey, P.V. Tobias and J.R. Napier in 1964.

Figure 7. Cranial capacity, means and estimated population limits, for each of five or six early hominid taxa. On each bar, the vertical line represents the sample mean, while the termini of each bar represent the 95 per cent population limits for the taxon/taxa indicated.



ESSENTIAL FEATURES OF THE HOMINIDS MORPHOLOGICALLY DEFINED

Le Gros Clark (1964), in his definition of the family Hominidae, listed 19 defining processes or complexes, all of which are such that their presence or absence can be verified on fossilized skeletal remains. Sixteen were cranial and dental; three were postcranial. Pilbeam (1968) simplified the listing to two principal sets of criteria: evidence of habitual bipedalism as the chief method of locomotion, and the presence of teeth which are essentially human in form.

Between these two extremes, I shall here specify seven major aspects of the hominid morphological pattern (Table 4).

The attainment of these seven complexes, in varying degrees, at different times, and by diverse rates of change, characterised those higher primates which became swept up in the evolutionary radiation known to us as hominization.

(a) The attainment of habitual and prolonged upright posture and habitual bipedal locomotion, namely standing, walking and running (Table 5). Far from being a simple set of changes, this complex involved (i) alterations in the structure of the base of the cranium and of the cranio-vertebral alignment; (ii) development of structural mechanisms for the transmission of weight down the spinal column, through the upper part of the sacrum, to and through the ilium of the hip-bone; (iii) substantial modifications of the pelvis which made the new locomotor mechanism possible without the sacrifice of the other primal function of the pelvis, namely to serve as the birth canal; (iv) adjustments in the head and neck of the femur, in the length, curvature and form of the femur, in the mechanism of the knee-joint, and in the ankle, foot and toes.

TABLE 4

Characteristics of Morphological Hominids

1) Upright Posture and Bipedal Locomotion
2) Re-structuring and Re-deployment of Upper Limb
3) Dental Changes
4) Allometric Enlargement of Brain and Neurocranium
5) Differential Enlargement of Certain Well-defined Areas of the Brain
6) Re-modelling of Cranium Including Mandible
7) Development of Structural Basis of Articulate Speech

All the fossil evidence goes to indicate that elements of this bipedalism complex were developed very early in the history of hominization.

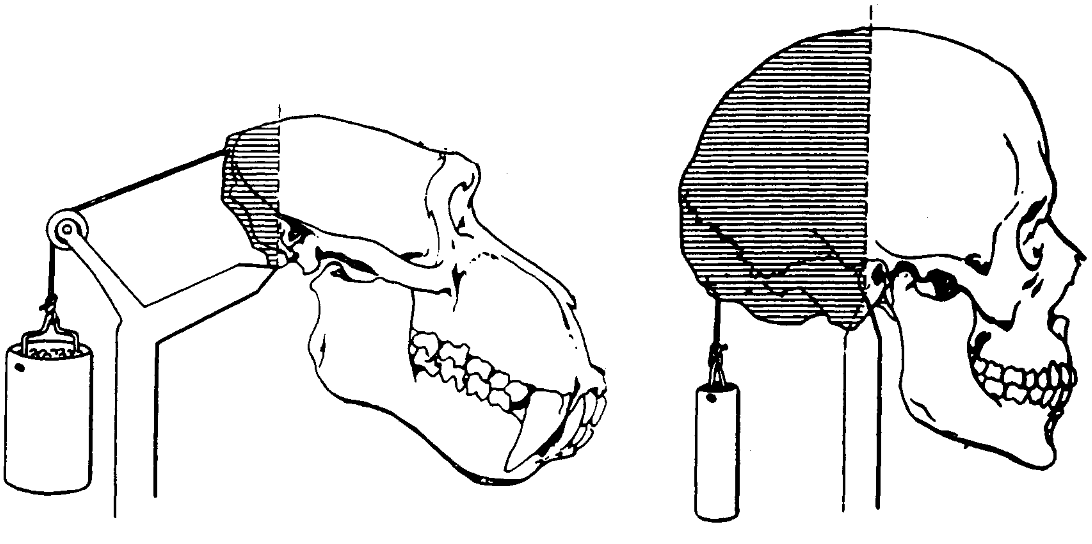


Figure 8. Skulls of baboon (left) and man (right). The suspended weights illustrate the difference in muscular bulk and strength required to hold the head on the vertebral column in such a position that the eyes would have been able to look straight to the front. In each instance the hatched part of the cranium is the proportion that lies behind the point of pivot on the spinal column. The tapering support shows the orientation of the spinal column and the position of its articulation with the cranium. Diagram by Th. Mollison, 1932.

TABLE 5

Changes in the Attainment of Upright Posture and Bipedal Locomotion

---

(a) alterations of base of cranium

(b) alteration of cranio-vertebral alignment

(c) structural mechanisms for transmission of weight
  -down spinal column
  -through upper part of sacrum
  -through ilium of hip-bone

(d) great modifications of pelvis

(e) adjustments of
  -head and neck of femur
  -length, curvature and form of femur
  -structure and mechanism of knee-joint
  -ankle, foot and toes

(b) The re-deployment and restructuring of the upper limb, from an organ involved in weight-bearing, standing, walking or running in a quadrupedal gait, or in brachiation, or in both, to one freed to a large extent or completely from locomotor activities and concerned with increasingly precise manipulation, involving *inter alia* shortening of the whole limb, elongation of the thumb and development of its functional anatomical property of opposability.

(c) Dental hominization (Table 6) — overall reduction in the size of the teeth, the jaws and the rest of the masticatory apparatus, differential diminution of the canine teeth from large fangs to relatively small teeth, whose tips are aligned almost on a level with those of the neighbouring teeth in the dental arcade; transformations of other teeth, affecting crown form, structure, shape, enamel thickness, absolute and relative crown size (including changes in dental step-index values — i.e., in the sizes of some teeth in relationship to those of other teeth), extent of pulp cavity, root number, form and structure; and changes in the patterns of occlusion and mastication.

TABLE 6

Types of Change in Dental Hominization

---

a) Relatively reduced canine teeth

b) Changes of
  -Crown Form
  -Crown Structure
  -Crown Shape
  -Enamel Thickness
  -Absolute and Relative Crown Size
  -Extent of Pulp Cavity
  -Root Number, Form, Structure
  -Occlusal Pattern
  -Masticatory Mode

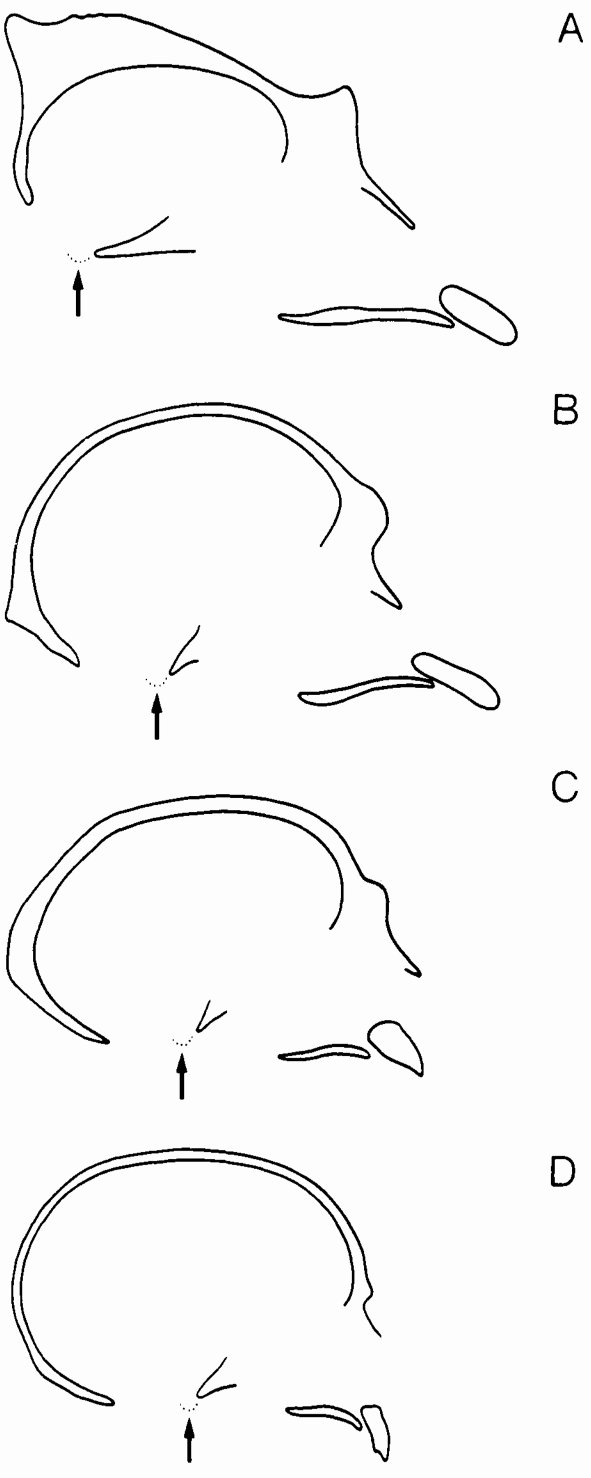


Figure 9. Median sagittal sections through the crania of gorilla (A), *Australopithecus africanus transvaalensis* (B), *Homo erectus* (C) and *Homo sapiens* (D). The position of the foramen magnum is clearly seen. The arrow points in each instance to the position of the maximum inferior convexity of the occipital condyles, as projected on the median plane. The diagrams show differences between ape and man, as well as a difference in the position of the condyles. There has been a forward 'migration' from ape to man and the position in *Australopithecus* is intermediate.

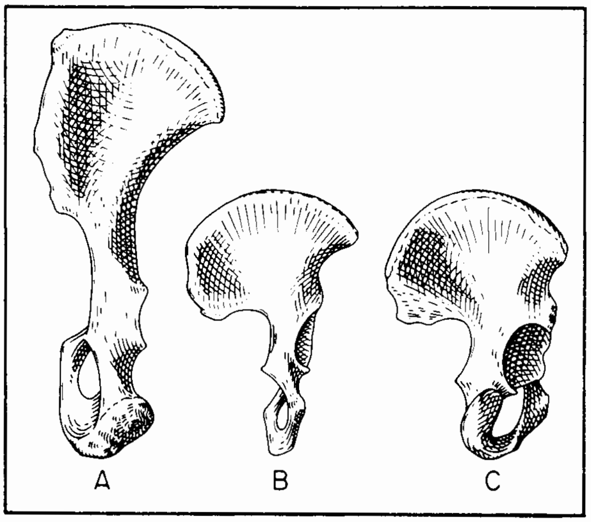


Figure 10. Right ossa coxae (innominate bones) of chimpanzee (A), *Australopithecus africanus* (B) and modern man (C). In each instance, the bone is oriented with the plane of the ilium at right angles to the line of sight, and with the anterior superior iliac spine pointing to the viewer's right. The transversely expanded ilia of man and *Australopithecus* contrast with the narrow, vertically expanded ilium of the ape.

(d) Gross encephalization — the strong positively allometric enlargement of the whole brain and concomitantly of the capacity of the brain-case.

(e) Selective encephalization — the differential development of certain parts of the brain, so that some areas with well-defined functions became preferentially enlarged more than others (especially the parietal and frontal lobes of the cerebrum, the posterior part of the inferior frontal convolution — Broca's area — and Wernicke's area), development of moderate to marked asymmetry of special parts of the cerebral hemispheres, particularly the post-rolandic part of the lateral (Sylvian) fissure and related areas.

(f) The re-modelling of the detailed morphology of the skull, including the mandible (Table 7), in accordance with (i) the re-positioning of the head upon an upright spine, involving changes in the cranial base and cranial poise, (ii) the changes in size of the dentition and masticatory habit and vigour, and (iii) the enlargement and re-modelling of the brain.

TABLE 7

Features of
Cranial Hominization

Re-modelling of Cranium in Accordance with:-

-Changes of Basis Cranii and Cranial Poise
-Dentition, Masticatory Habit and Vigour
-Enlargement and Re-modelling of Brain

(g) The development of articulate speech, a functional and behavioural trait with a structural underlay, requiring both (i) the development of the speech areas of the central nervous system, and (ii) peripheral changes in the airway and foodway, so as to form a vocal tract (Table 8a and 8b).

TABLE 8(a)

The Structural Basis of Speech

(a) *Central*	-Expansion of specific cerebral areas -Broca's Area -Wernicke's Area -Supplementary Motor Area Ms II

TABLE 8(b)

The Structural Basis of Speech

(b) *Peripheral*	-Modification of Upper Respiratory Tract to become a Vocal Tract - loss of intimate contact between epiglottis and soft palate - laryngeal aditus comes to face posteriorly - continuity between nasal cavities and larynx interrupted by foodway - oral airway supplements nasal airway - appearance and expansion of nasopharynx - 'descent' of larynx

With these seven broad modalities of hominizing change in mind, we may examine the fossil record, not losing sight of all its imperfections to which, in general terms, Charles Darwin drew attention, and, in which blemishes are still with us, despite the exponential increase in the treasury of fossils.

PATTERNS AND PROBLEMS OF HUMAN EVOLUTION

Although there is still some dispute, often exaggerated, among paleo-anthropologists on what names to give to new specimens and how to view the pattern and timing of hominid change, a general consensus has emerged in recent years that the hominid tree of descent has been Y-shaped. That is to say, there was at one time an essentially single lineage of hominids (the stem of the Y). Then there occurred one of those great evolutionary events, the splitting of a lineage (or cladogenesis). In my analysis of the fossils, this seems to have occurred just under 2.5 million years ago; though on the view of White, Johanson and Kimbel (1981) it had already taken place before the time of the Makapansgat and Sterkfontein *A. africanus* fossils (i.e., perhaps earlier than 3.0 mya). Although I do not believe that the evidence supports their interpretation nor that their version of the dating of the Transvaal fossils is correct, the Y-pattern is explicit in their scheme as well. After the split, one arm of the Y led to the robust and hyper-robust australopithecines, while the other arm gave rise to the genus *Homo*. For at least another million or more years the two derivative stocks co-existed in Africa, in the form of *Homo habilis* and then *Homo erectus*, on the one hand, and of the late-surviving robust australopithecines, on the other hand. Eventually, about one mya, the line of the robust australopithecines became extinct and only the other arm of the Y persisted, giving rise subsequently to *Homo sapiens*.

This basic pattern raises many interesting problems of speciation and cladogenesis (the splitting of a lineage) and in the ensuing section of this presentation, I shall examine some of these.

(a) Hominid Cladogenesis

The cladogenesis our analysis has unearthed occurred about 2.5 mya. At that time there lived in Africa an ancestral species of hominid, *A. africanus*, with several local subspecies in South and East Africa. Probably a little less than 2.5 mya, this species underwent a cladistic branching. Some populations went on developing in what one might regard as an orthodox mammalian fashion, with general enlargement of body size and, concomitantly, of teeth, jaws, brains, muscles and bones. These branches, with a definite morphological gap between the South and East African phases, appeared between 2.5 and 2.0 mya. The resulting 'robust australopithecines' persisted until about 1 mya, that is, they lasted for between 1 and 1.5 million years.

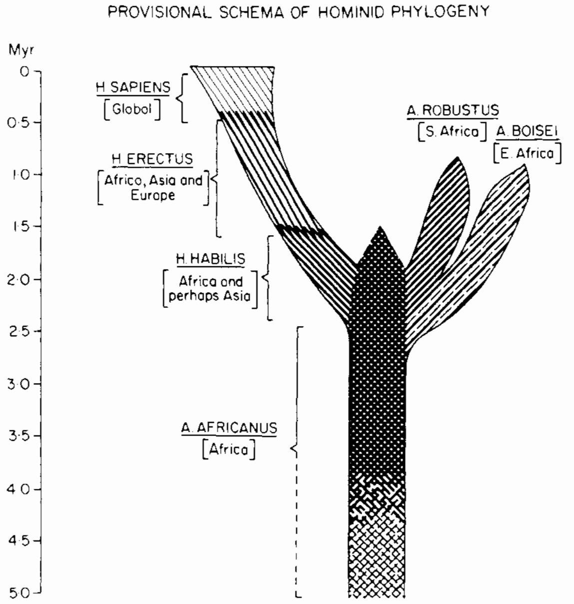


Figure 11. Schema of hominid evolution over the last five million years. The diagram illustrates an important point of cladogenesis, or the splitting of a lineage into two or more lineages, some 2.3 million years B.P. After this cladistic branching or 'punctuation' one of the major derivative lineages — that of the genus *Homo* — underwent considerable further change over the ensuing two million years, from *H. habilis* through *H. erectus* to *H. sapiens*. This part of the hominid phylogenetic tree illustrates what has been called phyletic gradualism, while the last 1.0-1.5 million years along this lineage, it is suggested, was characterised by a third pattern of change, namely reticulate evolution.

About the same time, just less than 2.5 mya, other populations of *A. africanus* started to develop in another direction to produce early *Homo*. This branch was marked by decided moves in the direction of later man: moves such as cerebral enlargement, dental diminution, many other detailed morphological changes, leading even to a new way of occluding and attriting of the teeth. Quite early along this atypical branch, stone cultural remains appeared in association with the skeletal specimens. A new dimension had been entered in human evolution, and this novelty itself must be assumed to have played an ever-increasing role in the further stages of the evolutionary process. Very probably this cultural innovation elicited the 'temporary intensification of selection' to which Rensch attributes such explosive events of evolutionary radiation.

(b) Ancestral and Non-ancestral Hominids

It was once rather facilely held that all earlier hominids were ancestral to later hominids. Despite widely diverging morphologies, all manner of hominid fossils from the late Tertiary and early Quaternary epochs were forced into a Procrustean bed of a single hominid lineage. Where near-contemporary fossils differed markedly, the diversity was liable to be attributed to sexual dimorphism, or high individual variability. There is now a wide consensus that some of the earlier fossil hominids were ancestral to later ones, whilst others were not and represented side-branches.

The first evidence that not all of the early hominids were ancestors of the later ones came into the hands of Robert Broom in 1938 when he found a different, more robust kind of ape-man at Kromdraai close to Sterkfontein where, two years earlier, he had found the first adult australopithecine of a more slender build. Although such a phenomenon is commonplace in the paleontology of other animals, in anthropological studies, it had until that moment seldom if ever been realised that early hominids had diversified and speciated cladistically — that is by branching; nor that some of the branches — which were legitimately classified as hominid — were not ancestral to later man of the genus *Homo*.

(c) The Extinction of Some Early Hominids

Another important conceptual development is that, not merely had the early hominids speciated by divergence at a certain stage in their phylogenesis, but one or more of the branch-lines had actually become extinct. Such an idea had on several occasions been put forward in respect of Neanderthal man in Europe, namely that it was a side-branch that died out. But the evidence for such suggested Neanderthal extinction has never been convincing and Middle European intermediates between Neanderthals and later *Homo sapiens* fossils have largely given the quietus to this view. In the case of the earlier hominids, however, it is now clear that the South African fossils of *Australopithecus robustus* from Kromdraai and *Australopithecus robustus crassidens* from Swartkrans, and *Australopithecus boisei* of East Africa became extinct about one mya. Yet all were good hominids on all accepted classifications.

(d) The Claims of Africa and Asia

An emphasis on Asia as the cradle of mankind had gained wide credence in the first quarter of the present century. The discoveries of Dubois in Java (Indonesia) and a few finds in China had led to this belief. These earliest Asian hominids are now generally classified as *Homo erectus*. The African finds from 1925 onwards have thrown up earlier hominids of a less specialised kind, such as those we classify today in *Homo habilis* (Leakey, et al. 1964) and in one or other of the several species of *Australopithecus*. Not only are these forms more primitive hominids than those recognised in Asia, but they are earlier in time. Thus, the most reasonable interpretation of the available evidence now is that the hominid family took its origin in Africa. Indeed, these finds in Africa over the past 57 years have corroborated an old prophecy which Charles Darwin made in his 1871 book, *The Descent of Man*, namely–

> In each great region of the world, the living mammals are closely related to the evolved species of the same region. It is, therefore, probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and chimpanzee; and, as these two species are now man's nearest allies, *it is somewhat more probable that our early progenitors lived on the African continent than elsewhere.* (italics mine).

This remarkable and relevant prediction was based by Darwin on the evidence of comparative anatomy which had shown the African great apes to be "man's nearest allies". The fossil evidence to prove this view was lacking in 1871. That is why, in the next sentence, Darwin added, "But it is useless to speculate on the subject." Dart's discovery in 1925, and all those that followed, translated Darwin's inference into a verified deduction.

(e) Variations and the Recognition of New Species and Genera

Earlier analyses of the fossil record were most intolerant of variations. When the number of fossils available was still small, there could obviously have been little appreciation of the ranges of variation within a species. The difficulty was compounded because few detailed comparative studies had at that time been made on the variability of the bones of the living higher Primates, except for those of man. Little was known about the variability of living gorillas or of living chimpanzees in observable, metrical traits. Hence, a relatively narrow margin of difference between two fossils was likely in earlier days to lead to their being classified as members of two different species or even of two genera. Thus, at one time or another, African fossils of the so-called australopithecine grade of structural organisation have been classified in no fewer than seven different genera, *Australopithecus, Plesianthropus, Paranthropus, Meganthropus, Praeanthropus, Zinjanthropus* and *Paraustralopithecus*. Broom at one stage went so far as to classify the South African australopithecines alone into three different sub-families.

With the accumulation of more specimens, greater insights grew into the nature and extent of sex-differences, age-changes, individual variations, and regional and temporal variants. The analysis of such 'fossil populations' was greatly assisted by the concomitant study of variance within living populations of the extant higher primates (Table 9). The newer approach was accompanied by ever-increasing refinements of statistical methods and especially of multivariate analysis. It led to a stress on population biology of the fossil hominids and to a simplification of the classificatory devices employed.

Variability and the Reduction in the Number of Species and Genera

There is a wide consensus today that all of the small-brained early hominids, formerly classified in up to seven genera, should be accommodated within a single genus *Australopithecus*. A handful of workers retain two genera of australopithecines. In a similar way the Neanderthalers of Europe, Asia and North Africa have at various times been classified in a differ-

TABLE 9

The Variability of Hominoid Cranial Capacities

Species	Size of Sample	Mean	Difference between maximum and minimum values (c.c.)	Estimated standard deviation (c.c.)	Estimated coefficient of (%)
Gibbon	86	94.3	43	7.17	8.0
Siamang	40	124.6	52	8.67	7.0
Chimpanzee	144	393.8	160	26.67	6.8
Orang-utan	260	411.2	180	30.00	7.3
Gorilla ♂ + ♀	653	506.0	412	68.67	13.6
Gorilla ♂	400	534.8	332	55.33	10.4
Modern man	-	± 1344	± 1000	166.67	12.4

ent genus (*Palaeoanthropus* or *Protanthropus* or *Prothomo*) from that of modern man (*Homo*); then as a different species (*Homo neanderthalensis, H. primigenius, H. europaeus, H. mousteriensis* or *H. antiquus* etc.) as distinct from *H. sapiens*; and most recently as a different race or sub-species (*H. sapiens neanderthalensis*) in contrast with *H. sapiens sapiens*. Many current arguments over the systematic status of various newly-found African fossils are simply the consequence of varying judgements by paleo-anthropologists as to whether the morphology and morphometrics of the new finds can or cannot be accommodated within an existing, previously defined species. More detailed study of the specimens and their careful comparison with previously known fossils, as well as the discovery of more specimens and enlargement of sample-sizes, usually leads sooner or later to a resolution of such differences. For a time, though, arguments at this level seem to monopolize the intellectual and emotional energies of the protagonists! It is important, though, for us to keep a sense of proportion about the relative importance, or lack of importance, of such differences of opinion. In such altercations, the key differences often do not reside in the fossils themselves, but in the powers of observation of the discoverers, the accuracy of their measurements, their familiarity with other comparable fossil collections and their morphological acumen.

(g) The Exaggeration of Differences

A corollary of the last item is that there has been a long-lasting and oft-criticised tendency of discoverers of fossils to exaggerate the differences between the newly-found specimens and those found earlier and by other workers. With this has gone a decided tendency to create new species over-readily. Thus, the history of paleo-anthropology is littered with the names proposed for imagined new species. Most of these are rapidly discarded and remain only as historical reminders, often romantic and fanciful rubrics in the chronicles of the discipline. Sometimes the name reflects more about the nature and personality of the discoverer than about the affinities of the specimens to which the appellation refers. This tendency to multiply names might be dismissed as an amusing sidelight on the history of paleo-anthropology, were it not that it has too often cluttered the field, masked the relationships, perhaps delayed the evaluation of the specimen's affinities, and alas, plagued the life of the earnest student of the subject.

It would be gratifying if one were able to report that this trend has come to an end. Unfortunately, it seems to be lingering on and at least three or four new species have appeared on the marketplace in the last seven years (*A. afarensis, A. crassidens, Paranthropus africanus, Homo ergaster*). Of course, as paleontologists venture into previously unsampled time-levels, it becomes increasingly likely that new taxa may come to light: but the final judgement on the classificatory designation of a sample of fossils must remain morphological appraisal, irrespective of the time dimension. Indeed, the study of fossil hominids is primarily a paleo-anatomical problem; the *evaluation of the place and significance* of those fossil hominids requires in addition the insights of taphonomy, geochronology, zoogeography, paleo-ecology, ethology, taxonomy and, where applicable, archaeology.

(h) Continuous or Discontinuous Change?

Another concept that has been changed by the accumulation and classification of new fossils is the idea that change throughout the evolution of the Hominidae was virtually continuous. This *idêe fixe* was encouraged by the principles and conventional wisdom of human population genetics. It was this notion that was responsible sometimes for the dismissal of certain fossils as 'too specialized' to have been on the main line of evolution. The belief in continuous change in paleontological studies in general has been designated as 'phyletic gradualism'. If it was tacitly or overtly assumed that such had been the pattern of hominid phylogenesis, the close morphological appraisal and dating of the masses of newly discovered fossils, especially in Africa, have shown in no uncertain terms that the pattern has been quite different.

It seems that there have been fairly lengthy periods of gradual change, but that at one or two points there has been a phase of virtually explosive radiation of the ancient hominids. For example, between 2.5 and 2.0 mya, there is much evidence to suggest that a previously single hominid lineage underwent cladogenesis or a splitting into several lineages. Thus the earlier line of *A. africanus* gave way to at least two and possibly several lines — those of *A. robustus* in South Africa (including those regarded as a separate species, *A. crassidens*, by Howell 1978), *A. boisei* in East Africa, *H. habilis* in East and South Africa and, possibly a temporary continuation of the line of *A. africanus* itself. Such a node along the pathway of hominid evolution, separating consecutive periods of more gradual, non-cladistic change, illustrates the pattern which in the last decade has come to be known as the concept of 'punctuated equilibrium' (Eldredge and Gould 1972).

After the particular node just mentioned, the pattern of change along the line of evolution of *Homo* lends itself variously to analysis in terms of phyletic gradualism, punctuated equilibrium or reticulate evolution (Tobias 1978).

(i) Gradualism or Punctuated Equilibrium?

From the preceding comments, it might seem tempting to interpret the pattern of hominid evolution as illustrating the Eldredge-Gould model of punctuated equilibrium (1972, 1977). Such an interpretation is seriously questioned in the next section, but even if it is here accepted for purposes of discussion, the evidence does not support the important corollary of the Eldredge-Gould viewpoint, namely their claim that the main significant steps in evolution take place at branch points and that what happens before and after is of relatively minor importance. This is certainly not true of the hominids. For instance, there is no doubt that the lineage of *Homo* after its cladistic origin underwent most remarkable and significant changes through a phyletic sequence of three consecutive chrono-species. The linking of these consecutive chronospecies in a single lineage (*H. habilis*→*H. erectus*→*H. sapiens*) was first proposed by the author in 1967; it has been supported most recently by White, Johanson and Kimbel (1981), though the latter authors draw attention to Gould's (1979a) comment that such linking implies more gradualism in later human evolution than he is prepared to accept! The late changes were especially marked in respect of brain-size, tooth- and jaw-size and the appearance of the anatomical basis of articulate speech. These traits developed during hominid phylogeny in a mosaic fashion — that is different traits showed differing rates and times of change within a single lineage or even between closely related lineages.

(j) The Case for Phyletic Gradualism in the Evolution of Quaternary Hominids

If one considers individual hominid traits, the case for gradualism of change after the explosive radiation and speciation of ca 2.3 mya is very strong indeed. In the ensuing 1.5 to 2.0 million years, brain size more than doubled — from an average of 645 cm^3 in *Homo habilis* to a mean cranial capacity of ca 1345 cm^3 in modern man, irrespective of race or sex. The modern brain-size seems to have been reached some time ago, perhaps 100,000 years ago. The cerebral expansion appears to have affected all of the human population on a world-wide basis; it was not an isolated or peripheral phenomenon (Coppens 1981; Tobias 1970, 1971a, 1971b, 1975b, 1980b, 1981a). This remarkable amount of change in brain-size occurred without evidence that the successive populations of *Homo* were speciating by nodal radiation at any points along this lineage. This example tends to contradict the view of Gould and Eldredge (1977) to the effect that gradualism is not evident in the paleo-anthropological record, a view that Brace has described as 'bold but unsupported' (1981: 422). Another, perhaps equally dramatic change that has occurred in the same time period relates to the diminution of tooth size. In the hands of Brace's analysis (1979), human tooth size 'has reduced by a full 50% in a broad belt running from Europe to Japan' (Brace 1981: 422). My own studies revealed a reduction in tooth material (values for summed crown areas of mandibular cheek-teeth) from 787 in *H. habilis* to 484 in modern *H. sapiens* (world-wide inter-population mean): that is a reduction of about 40% on the *H. habilis* value (Tobias 1981b). Brace's and my figures are very similar and bespeak a most striking reduction in the mean size of the cheek-teeth over a period of 1.5 to 2.0 million years. Yet, this reduction has been world-wide (though in varying degrees) and has taken place without manifest evidence of punctuating nodal events.

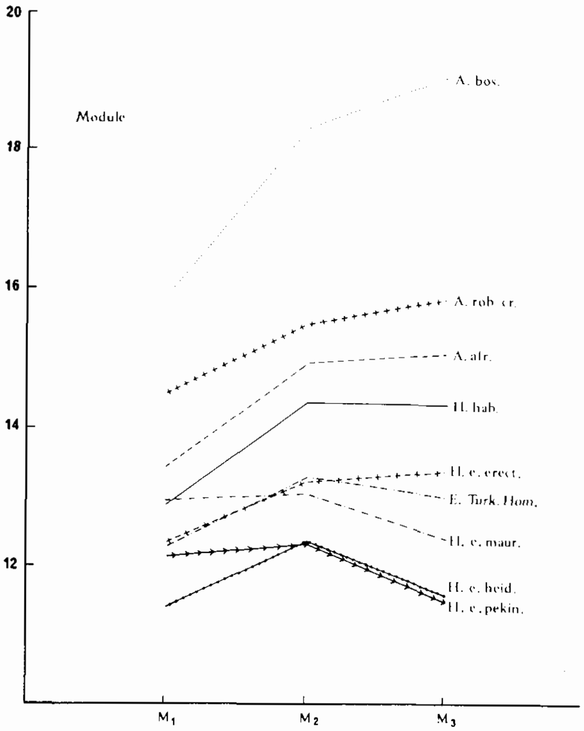


Figure 12. The sizes of the crowns of the lower three molars of the permanent dentition of early hominids. For each named taxon, the sample means for crown module (half the sum of the mesiodistal and the buccolingual diameters) are given for the three molars. The graphs show the clear and marked tendency to reduction of molar size from *A. africanus* through *Homo habilis* and through a variety of geographical subspecies of *H. erecuts*. In the other direction, the 'robust' lineages stemming from the cladogenetic event of 2.3 million years B.P. show marked increase in molar crown size.

A. bos.	-*Australopithecus boisei*
A.rob.cr.	-*A. robustus crassidens* of Swartkrans
A.afr.	-*A. africanus transvaalensis* of Sterkfontein and Makapansgat
H.hab.	-*Homo habilis*
H.e.erect.	-*Homo erectus erectus* of Java, Indonesia
E.Turk.Hom.	-mixed east Turkana hominids, probably comprising specimens of *H. habilis* and of *H. erectus* (not yet specifically identified)
H.e.Maur.	*H. erectus mauritanicus* from northwest Africa
H.e.heid.	*H. erectus heidelbergensis* of Mauer, Heidelberg, Germany
H.e.pekin.	*H. erectus pekinensis* of Choukoutien

These and other lines of metrical evidence show that, since the last major punctuation in hominid evolution (at about 2.3 mya), phyletic gradualism with speciation has been evident in the paleo-anthropological record. The data lead me to support Brace's (1981) claim that the data of paleo-anthropology show that gradual change does occur in the supposed 'equilibrium' phases between 'punctuations.' It begins to look as though hominid evolution exhibits neither 'punctuated equilibria' alone, nor phyletic gradualism alone, but shows at different times dramatic nodal events (like the explosive hominid radiation of 2.3 mya) and slow gradual changes which in their total effect are far from minor. Although the tempo of these gradual changes may be slower than at the points of explosive radiation, their cumulative effect must be adjudged no less dramatic. The brain changes, for instance, made possible the emergence of, and progressive dependence upon, human material culture, as well as the evolution of articulate speech — probably the two most significant features in hominization, after the attainment of the upright posture and bipedal locomotion.

We may thus see hominid evolution as proceeding at different rates at different times, a conclusion to which also Cronin, et al. (1981) have been drawn. It does not provide an illustration of the punctuated equilibrium model in its full exposition. It is of course not the only example of a well-documented phylogenesis that is at variance with the Eldredge-Gould model. Bookstein, Gingerich and Kluge (1978) have worked out the relative fit of the hypotheses of phyletic gradualism and punctuated equilibria to two sets of temporally ordered metrical data, namely the size of the first molar of the primate *Pelycodus* and of the condylarth *Hyopsodus*: in 17 tests of the two data sets, they discovered 12 instances of gradualism, four of punctuation and one of equilibrium. On the other hand, as Kennedy (1981) has pointed out, the best examples of the punctuated equilibrium process have been found among marine invertebrates whose hard exoskeletons allow abundant representation in the fossil record and permit the preservation of more or less whole individuals. The instances cited are radiolarians (Kellog and Hays 1975), ammonites (Reyment 1975), trilobites (Henry and Clarkson 1975) and brachiopods (Ager 1973).

Perhaps, for terrestrial vertebrates, where emigration, immigration and marked geographic variation are striking features, the truth may lie somewhere between the two extremes, as it appears to do in the case of hominid phylogenesis.

(k) Darwinian or Non-Darwinian?

It is important to bear this in mind, becuse it is understood by many that gradualism is inherent in Darwinian theory, while it is averred that stepwise evolution is inherent in the cladistic approach (which is related to, though not synonymous with, the proposition of punctuated equilibrium). This emerged clearly in the correspondence in the columns of *Nature* over the last year or two, as reviewed recently by the President of the Royal Society, Sir Andrew Huxley (1982). Huxley has been at pains to point out that the proposition of punctuated equilibria is not at all at variance with Darwinian thinking, and he cites chapter and verse from Darwin's own writings to corroborate this interpretation. Indeed, neither is it at odds with the so-called neo-Darwinian synthesis, and he quotes Abel (1929), Simpson (1944, 1953) and Julian Huxley (1957) as witnesses to this viewpoint. It represents but one of Julian Huxley's modes of evolution. The 'punctuations' correspond to the steps of 'quantum evolution', so named by Simpson (1944, 1953); the equilibria correspond to Julian Huxley's 'stasigenesis' (1957) under control of what Schmalhausen (1949) and Mather (1953) called 'stabilizing selection'. Indeed, Andrew Huxley (op. cit.:xii) reminds us that Darwin himself drew attention to periods of stability postulated for each species (such as the equilibria posited on the punctuated equilibrium model). In the first edition of the *Origin of Species* (p. 118), Darwin stated,

> 'But I must here remark that I do not suppose that the process ever goes on so regularly as is represented in the diagram, though in itself made somewhat irregular.'

However, in the fourth (1866: 132) and later editions, he added that neither did he suppose "that it goes on continuously; it is far more probable that each form remains for long periods unaltered, and then again undergoes modification." In another part of the fourth edition (pp. 359-360), Darwin said, with an acknowledgement to Falconer, that "the periods during which species have been undergoing modification, though very long as measured by years, have probably been short in comparison with the periods during which these same species remained without undergoing any change."

Thus, Darwin himself referred to what has been called recently the theory of punctuated equilibria! Hence, it is not at variance with Darwinian thinking or the neo-Darwinian synthesis, as some have held: it simply represents a special emphasis on one part of Darwinism.

(l) Rate of Change and Phyletic or Cladistic Events

One point which seems to be at variance between Darwinism and the proposition of punctuated equilibria is that, for Darwin, the nodes or punctuations were periods of accelerated modification of a species. For Eldredge and Gould they were periods of accelerated modification by branching or cladistic splitting of a species into two (or more) species. The branching or cladistic emphasis appears to be an essential component of their theory and seems, in their thinking, to have been inextricably interwoven with accelerated change. Darwin envisaged periods of rapid change which were not *necessarily* associated with branching events: they might or might not have been, depending on the individual circumstances of each species. Or, to put it in another way, some instances of rapid modification might have arisen by branching events with speciation, whilst others might have arisen phyletically, without major cladistic phenomena. Thus, Darwin's system allowed for rapid change with either cladistic or phyletic evolution; whereas that of Eldredge and Gould appeared to stress cladistic evolution, almost to the total exclusion of phyletic evolution. The story of hominid evolution shows what appears to be clear evidence of at least one phase of cladistic evolution (notably the cladogenesis of 2.3 mya) and other periods, possibly one earlier and most probably one later than that, of phyletic change. In this respect, the Darwinian pattern seems to be more versatile and to fit the facts of hominid paleontology better.

(m) Speciation and Cladogenesis

To my understanding of the views of Eldredge and Gould (1972), most speciation requires a cladistic event to occur — so that one part of a species' range diverges from another part. They appear not to have countenanced the possibility that speciation has often occurred, through appropriate environmental change, without the splitting of a line. It would appear to me, from my study of hominid phylogeny, that speciation might occur with or without cladogenesis (the splitting of a lineage — Simpson 1953; Rensch 1959); but that cladogenesis cannot occur without speciation. As Simpson (1953: 380) has pointed out, speciation is the basic mechanism of the splitting of lineages. At the lowest level, the process of speciation "starts with differences between individuals, which in the most local population groups are usually very minor and fluctuate from generation to generation..." The intriguing question is, of course, what factors are responsible for cladogenesis, or for a moment of explosive evolution. For therein may be sought, and perhaps be found, the nature of the 'initial kick' which led to the debouchment of hominine life and culture. In broad terms, Rensch (1959: 112) said of this question,

> The essential factor in the causation of such periods of explosive radiation is not an increase of the rate of mutation or an accumulation of macro-mutations, but an acceleration of differentiation, brought about by a temporary intensification of selection due to environmental changes, e.g., by new types of vegetation or food resources, or due to the colonization of new ranges with habitats unoccupied or inhabited by types inferior in competition.

Of course, to claim that cladogenesis cannot occur without speciation is not to overlook cases of what one might call incomplete cladogenesis or incomplete splitting of a lineage. In such a case, the splitting events, if accompanied by minimal divergence, might be succeeded by convergence. This might possibly have happened in the case of *Homo erectus*: branching events might well have occurred, leading to such micro-taxa as subspecies or geographical races. Before the divergence could have proceeded too far, re-convergence might have supervened. The overall effect might well have been a pattern of reticulate evolution (Tobias 1974b, 1978).

(n) Reticulate Evolution in Quaternary and Recent Man

Julian Huxley (1963) has drawn a careful distinction between two different kinds of reticulate evolution based on two different mechanisms. It is well to recall his words here, since reticulate evolution is not often mentioned these days, when so much emphasis falls on the two supposed alternatives of phyletic gradualism and punctuated equilibria. Huxley's characteristically incisive analysis led him to distinguish between what he called the 'convergent-divergent' type of reticulate evolution, such as has been inferred to have occurred in roses, brambles, willows and hawthorns, and the 'recombinational' type which Huxley assigned to man:

> Here (in man), a reticulate result has been achieved by quite other means. Instead of the initial crossing being between distinct species, and the divergent variability being due to segregation of whole chromosomes or genomes, the crossing appears to have taken place between well-marked geographical subspecies, and the divergent variability is thus due to ordinary gene recombination. So far as we know, no polyploidy and no formation of specially stable types has occurred, but the progressive increase of general variability...
>
> Man is the only organism to have exploited this method of evolution and variation to an extreme degree, so that a new dominant type in evolution has come to be represented by a single world-wide species instead of showing an adaptive radiation into many intersterile species. Doubtless this is due to his great tendency to individual, group, and mass migration of an irregular nature, coupled with his mental adaptability which enables him to effect cross-mating quite readily in face of differences of colour, appearance, and behaviour which would act as efficient barriers in the case of more instinctive organisms. (J. Huxley 1963: 353-354)

Julian Huxley was referring to such reticulate evolution especially in recent man. However, the very qualities of man, which Huxley believed have been and are responsible for his recent recombinational pattern of reticulate development, have almost certainly characterized the human line for hundreds of thousands of years, at least since the stage of *Homo erectus*, now widely considered to have been the immediate precursor of *Homo sapiens*. A pattern of reticulate evolution seems to have characterised *Homo erectus*, during the Middle Pleistocene: this inference is based upon an interpretation of the fossil record of the time. The earliest members of *H. erectus* have been assigned an age of about 1.5 mya, based on East African discoveries (R.E.F. Leakey and Walker 1976). It is possible that reticulate evolution characterised the human line throughout the Quaternary. It is of course taxonomically untidy and awkward to embrace this concept — already systematists have recognized a number of geographical subspecies of *H. erectus* (e.g., *H. erectus erectus, H. erectus pekinensis, H. erectus lantianensis, H. erectus mauritanicus, H. erectus heidelbergensis*, etc.). The very multiplicity of names and of proposed micro-taxa seems to support the reticulate nature of the evolution of *H. erectus*. Julian Huxley was well aware of this taxonomic difficulty with reticulate situations when he wrote, "There is a natural reluctance among systematists to recognize its existence and its implications, since these run counter to the generally-accepted basis of taxonomic practice" (op. cit.: 356). Nevertheless, if the fossil data point towards reticulate evolution, the taxonomic preconceptions and procedures should be no valid deterrent to the upholding of the concept!

(o) Dichotomies of Dental Evolution in the Hominids and in Homo

If we use the size of the tooth crowns of *A. africanus* as a base-line, we find that two trends become evident from about 2.5 mya onwards. In some hominids, *A. robustus* and *A. boisei*, the crowns of the cheek-teeth became greatly increased in size, the 'tooth material' increasing from a value of 861 in *A. africanus transvaalensis* to 960 in *A. robustus crassidens* of Swartkrans and 1312 in *A. boisei.* These are values for summed crown areas of mandibular cheek-teeth. In other hominids, those assigned to the genus *Homo*, there is a reduction in tooth material to 787 in *H. habilis*, 695 in *H. erectus* of Indonesia, 665 in *H. erectus* of Africa, 608 in *H. erectus* of China, 544 in *H. erectus* of Europe, and 485 in *H. sapiens* (world-wide inter-population mean). Thus, there is a dichotomy of dental evolution from *A. africanus* onwards.

There is, however, another dichotomy which the author's researches on the early hominids of Africa and Asia have revealed. Within the line of evolution of *Homo*, there seem to have occurred two different patterns of dental reduction from the stage of *H. habilis* onwards. In Africa we find a tendency towards buccolingual attenuation of the cheek-teeth, accompanied for a time by mesiodistal elongation, especially of the front cheek-teeth, the P3, P4 and M1, while the back teeth show mesiodistal truncation. This pattern of dental evolution tends to reduce overall masticatory surface area with some degree of elongation of the tooth row and a trend towards prognathism. In Asia, on the other hand, the earliest manifest tendency is for the cheek-teeth to become mesiodistally shorter, without losing their buccolingual expansion. This feature would tend to produce a shortening of the entire tooth row and a trend towards facial flattening. This Afro-Asian dichotomy suggests that the architectonics that mark the facial growth of African and Asian populations at the present time might have had much more ancient roots than was previously deemed likely.

A GLANCE AT BEHAVIOURAL HOMINIDS

In a previous study (Tobias 1975a), I drew attention to the fact that we may recognise *morphological hominids* (on which the classical zoological definitions of the Hominidae are based); *behavioural hominids*; *cytogenetical hominids*; and *molecular hominids*. For a human paleontologist, the fossil record throws no direct light on the early development of either the chromosomal or the molecular make-up of the hominids. It illuminates most revealingly the morphological attributes of putative ancestral hominids. As for the behavioural hominid, a large repertoire of traits distinguishes the hominid from the pongid (ape) family. This includes habitual, purposeful and patterned implemental activities (both the range thereof and dependence on them for survival): scavenging and hunting; loss of the oestrous cycle and its replacement by all-the-year-round sexual receptivity; the incest taboo; the gradual addition, to Bergsonian practical intelligence, of rational intelligence or the accrual, to Piagetian sensorimotor and pre-operational intelligence, of operational intelligence; the acquisition of articulate speech; the development of problem-solving abilities to a high degree; symboling and the organization of symbolates into coherent cultural entities; the development of material and non-material culture; marked immaturity at birth and for some appreciable time thereafter; prolongation of childhood and adolescence with later menarche, later dental eruption and later completion of growth and ossification; a longer life span and the occurrence of menopause; the development of the human female breast; behavioural flexibility and educability (partly after Montagu 1965).

It is clear from a study of this list that some hallmarks of the behavioural hominid may be inferred from the paleo-anthropological record: for example, the possiblity of articulate speech; the presence of signs of material culture, such as stone and bone tools, construction of walling, collection of red ochre and other mineral earths; the nature of intelligence as may possibly be gauged from the complexity of the preserved material culture (cf. Parker and Gibson 1979; Wynn 1981), and so on.

SPEECH AND CULTURE

Elsewhere, I have adduced evidence pointing to the possession by *H. habilis* of both the neural basis and the peripheral capacity for articulate speech, albeit of a rudimentary form (Tobias 1980b, 1981a).

The humanness of speech was commemorated nearly 24½ centuries ago by Sophocles in his play *Antigone*:

> Of all the wonders, none is more wonderful than man,
> Who has learned the art of speech, of wind-swift thought,
> And of living in neighbourliness.

Much more recently, the American anatomist, George Washington Corner, jocularly expressed a profound truth on the relationship between speech, brain and culture, when he declared that the only reason an ape does not speak is that he has nothing to speak about! To turn the question about, how much did *Homo habilis* have to speak about?

There is now little doubt that *H. habilis* possessed a stone toolmaking ability and that he was responsible for those cultural assemblages designated Oldowan (M.D. Leakey 1971). This lithic cultural phase was characterized by a predominance of tools known as choppers, while other forms recognized are proto-bifaces, polyhedrons, discoids, spheroids and sub-spheroids, heavy-duty and light-duty scrapers, burins and sundry other tools. Of the choppers, five types have been described: side, end, two-edged, pointed and chisel-edged (op. cit.: 264). To this variegated suite of tool-types must be added the evidence that *H. habilis* was capable of constructing some form of shelter in the form at least of stone walling. In addition there is an unconfirmed report that he appears to have collected red earths on some of his living floors at Olduvai. The implemental and constructional activities bespeak a complex culture. Inferences from the fossil and archaeological record have led to the claim that the culture of *H. habilis* included the aimed throwing of missiles, the butchery of large animal carcasses with stone tools, the transport of meat and other foods to a home base, delayed

Figure 13. *Homo habilis* in the Transvaal: an early provisional reconstruction of Stw 53, effected by Alun R. Hughes and Ronald J. Clarke. This specimen represents a fine cranium of early *Homo* found with stone tools *in situ* in Member 5 of the Sterkfontein Formation, in 1976. *Homo habilis* is known from the Transvaal, Tanzania, Kenya and Ethiopia and appears to have ranged in time from about 2.3 to about 1.6 million years B.P.

consumption, the sharing of food, and the distribution of the meat to adult and juvenile members of the group (M.D. Leakey 1971; Isaac 1978). These inferred activities imply various propensities and abilities which Parker and Gibson (1979), among others, have attempted to delineate. All in all, the cultural achievements, both those observed and those inferred, imply a high degree of intelligent activity and it could well be enquired whether such a culture could have been transmitted without some form of speech.

It may reasonably be supposed that there is a limit to the degree of complexity of behaviour and cultural life which may be transmitted without speech. Those behavioural traits and propensities of which the pongids have been shown capable are transmitted by observational learning and gestural activities. In these respects the apes have carried the mammalian potential for learned behaviour to a very high degree of development. Indeed, it would seem that among the mammals, the living great apes — and perhaps, by inference, *Australopithecus* — have carried non-verbalised learned behaviour to its highest pinnacle (unless it be that the giant marine mammals have gone as far or further). More complex procedures, which necessarily invoke abstract notions, a sense of the past and of futurity, require more than grunts, nudges, observation and imitation to transmit them to the next generation. When evidence of such complicated cultural mechanisms appears in, or may be inferred from, the paleontological and archaeological record, it becomes necessary to postulate the presence of a more efficient mechanism than example and imitation: one form of such a more efficient teaching mechanism is speech.

The complexity which archaeologists have shown in, or inferred from, the life-style of *H. habilis* seems to this author to mark the point at which adequate and efficient transmission of cultural practices and advances to the offspring required at least rudimentary speech.

At least two attempts have been made recently to evaluate the intelligence of *H. habilis* in terms of Piagetian genetic epistemology. In one, more limited study, Wynn (1981) has used the geometry of the artefacts of the Oldowan culture as a basis for his study. He admittedly employs a very narrow range of attributes (op. cit.: 529). He analyses only the features of the choppers, polyhedrons and scrapers from Olduvai and reaches conclusions about minimum necessary spatial concepts. From these, and from a recapitulationist use of Piaget's ontogenetically determined forms of intelligence, Wynn infers that the manufacture of Oldowan artefacts required only pre-operational organization. Such operations characterise pre-operational intelligence, the second of Piaget's three major stages in the ontogenetic sequence of intelligence he recognises (sensorimotor intelligence, pre-operational intelligence and operational intelligence, the latter marking the adult stage in modern human ontogeny). However, Wynn's analysis, it seems to this author, does not embrace the full range of cultural operations and tool types in the Oldowan; nor does it take within its purview the evidence of constructional activity, nor the patterns of behaviour that may be inferred from the living floors and the other archaeological records preserved.

When a more holistic picture of the life-style of *H. habilis* is used as a basis for the inference of habiline intelligence, such as has been attempted by Parker and Gibson (1979), a more advanced intelligence of *H. habilis* is perceived. The full gamut of pre-operational intelligence is seen to have been exploited, right to the threshold of the phase of operational intelligence. This appraisal of the intelligence of *H. habilis* sets him clearly ahead of the great apes, whose range of activities spans all the stages of sensorimotor intelligence and just reaches the level of pre-operational intelligence.

It could well be questioned whether Haeckelian recapitulationism may validly be applied to behavioural analysis of ancient hominids in the way attempted by both Parker and Gibson (1979) and Wynn (1981). The work of the former investigators has been criticized on this basis by Brainerd (1979), Dingwall (1979), Snowdon and French (1979), though supported by Gould (1979b). However, we at least have here some systematic attempts to analyse the evolution of human cognitive attainment. These attempts, added to the intuitive analyses in which the field of paleo-ethology abounds, give some support to the notion that, while *Australopithecus* had advanced functionally though not necessarily behaviourally over the apes, *H. habilis* had embraced a life-style of such complexity as to have led the author to raise the thought that its transmission would seem to have required speech.

Is it coincidence that the appearance of cultural complexification (to use Teilhard de Chardin's word) in the accomplishments of *H. habilis* was paralleled by the appearance of the cerebral bases for speech?

On this view, *H. habilis* had undergone an evolutionary transcendence, in the parlance of Dobzhansky (1967). The First Transcendence having been the origin of life itself, *H. habilis* underwent what Dobzhansky and Ayala (1977) called the Second Transcendence. By taking this great step forward, *H. habilis* had been enabled by its cerebral revolution to attain a new mode of evolution, as a speech-bound, culture-dependent hominid.

ACKNOWLEDGEMENTS

I extend thanks to the University of Alberta, to Professor Geoffrey Sperber, to Christel Eckert, Sally Wharton, Peter Faugust, Colin Richards, Alun Hughes, and others who have helped my researches on hominid evolution over many years.

REFERENCES

Abel, O.
1929 Paläobiologie und Stammesgeschichte. Jena: Fischer.

Ager, D.V.
1973 The Nature of the Stratigraphic Record. New York: John Wiley.

Bookstein, F.L., P.D. Gingerich and A.G. Kluge
1978 Hierarchical linear modeling of the tempo and mode of evolution. Paleobiology 4: 120-134.

Brace, C.L.
1979 Krapina, "classic" Neanderthals, and the evolution of the European face. Journal of Human Evolution 8: 527-550.

1981 Tales of the phylogenetic woods: the evolution and significance of evolutionary trees. American Journal of Physical Anthropology 56: 411-429.

Brainerd, C.J.
1979 Recapitulationism, Piaget, and the evolution of intelligence: dêja vu. The Behavioral and Brain Sciences 2: 381-382.

Ciochon, R.L. and R.S. Corruccini (eds.)
1982 Miocene Hominoids and New Interpretations of Ape and Human Ancestry. VIII Congress of the International Primatological Society, Italy, July 1982.

Clark, J. and T.D. White
1982 Press Release. University of California, Berkeley.

Clark, W.E. Le Gros
1964 The Fossil Evidence for Human Evolution. (2nd edn), Chicago: University of Chicago Press.

Conroy, G.C. and D. Pilbeam
1975 *Ramapithecus*: a review of its hominid status. *In*: R.H. Tuttle (ed), Paleoanthropology; Morphology and Paleoecology, Pp. 58-86. The Hague/Paris: Mouton.

Coppens, Y.
1981 Le cerveau des hommes fossiles. Comptes Rendus Académie des Sciences: 3-24.

Cronin, J.E., N.T. Boaz, C.B. Stringer and Y. Rak
1981 Tempo and mode in hominid evolution. Nature 292: 113-122.

Dart, R.A.
1925 *Australopithecus africanus*, the man-ape of South Africa. Nature 115: 195-199.

Darwin, C.
1859 Origin of Species. First ed. London: John Murray.

1866 Origin of Species. Fourth ed. London: John Murray.

1871 The Descent of Man. London: John Murray.

Day. M.H., M.D. Leakey and T.R. Olson
1980 On the status of *Australopithecus afarensis*. Science 207: 1102-1103.

Dingwall, W.O.
1979 Reconstruction of the Parker/Gibson "model" for the evolution of intelligence. The Behavioral and Brain Sciences 2: 383-384.

Dobzhansky, T.
1967 The Biology of Ultimate Concern. New York: New American Library.

Dobzhansky, T. and F.J. Ayala
1977 Humankind a Product of Evolutionary Transcendence. (Special Raymond Dart Lecture), Pp. 1-15. Johannesburg: Witwatersrand University Press.

Eckhardt, R.B.
1972 Population genetics and human origins. Scientific American 226(1): 94-103.

1973 *Gigantopithecus* as a hominid. In: R.H. Tuttle (ed), Paleoanthropology: Morphology and Paleoecology, Pp. 105-129. The Hague/Paris: Mouton.

Eldredge, N. and S.J. Gould
1972 Punctuated equilibria: an alternative to phyletic gradualism. *In*: T.J.M. Scopf (ed), Models in Paleobiology, Pp. 82-115. San Francisco: Freeman, Cooper.

1977 Evolutionary models and biostratigraphic strategies. *In*: E.G. Kaufman and J. Hazel (eds), Concepts and Methods of Biostratigraphy, Pp. 24-40. Stroudsberg, Pa.: Dowdan, Hutchinson and Ross.

Genet-Varcin, E.
1969 À la Recherche du Primate Ance7circumflex>tre de l'Homme. Paris: Boubée.

Gould, S.J.
1979a Our greatest evolutionary step. Natural History 88: 40-44.

1979b Panselectionist pitfalls in Parker and Gibson's model for the evolution of intelligence. The Behavioral and Brain Sciences 2: 385-386.

Gould, S.J. and N. Eldredge
1977 Punctuated equilibria: the tempo and mode of evolution reconsidered. Paleobiology 3: 115-151.

Henry, J.L. and E.N.K. Clarkson
1975 Enrollment and coadaptations in some species of the Ordovician Trilobite genus, *Placoparia*. Fossils and Strata 4: 87-95.

Holloway, R.L.
1975 Early hominid endocasts: volumes, morphology and significance for hominid evolution. *In*: R.H. Tuttle (ed), Primate Functional Morphology and Evolution, Pp. 393-416. The Hague: Mouton.

Howell, F.C.
1978 Hominidae. *In*: V.J. Maglio and H.B.S. Cooke (eds), Evolution of African Mammals, Pp. 154-248. Cambridge, Mass.: Harvard University Press.

Huxley, A.F.
1982 Address of the President Sir Andrew Huxley at the Anniversary Meeting of the Royal Society, London, 30th November, 1981. Proceedings of the Royal Society of London A 379:v-xx.

Huxley, J.S.
1957 The three types of evolutionary process. Nature 180: 454-455.

1963 Evolution: the Modern Synthesis (2nd edn with a new introduction), London: George Allen and Unwin.

Isaac, G.L.
1978 The archaeological evidence for the activities of early African Hominids. *In*: C.J. Jolly (ed), Early African Hominids, Pp. 219-254. London: Duckworth.

Johanson, D.C. and T.D. White
1979 A systematic assessment of early African hominids. Science 203: 321-330.

Kellog, D.E. and J.D. Hays
1975 Microevolutionary patterns in Late Cenozoic Radiolaria. Paleobiology 1: 150-160.

Kennedy, G.E.
1981 Macroevolution in the Hominoidea of the early Miocene. *In*: L.L. Mai, E. Shanklin and R.W. Sussman (eds), The Perception of Evolution, Anthropology UCLA 7: 113-131.

Leakey, L.S.B., P.V. Tobias and J.R. Napier
1964 A new species of the genus *Homo* from the Olduvai Gorge. Nature 202: 7-9.

Leakey, M.D.
1971 Olduvai Gorge, Volume 3: Excavations in Beds I and II 1960-1963. London: Cambridge University Press.

Leakey, R.E.F. and A.C. Walker
1976 *Australopithecus, Homo erectus*, and the single species hypothesis. Nature 261: 572-574.

Lewis, G.E.
1934 Preliminary notice of new man-like apes from India. American Journal of Science Series V, 27: 161-179.

Mann, A.E.
1968 The Paleodemography of Australopithecus. PhD. dissertation, University of California, Berkeley.

1975 Some paleodemographic aspects of the South African australopithecines. University of Pennsylvania Publications in Anthropology 1: 1-171.

Martyn, J.E. and P.V. Tobias
1967 Pleistocene deposits and new fossil localities in Kenya. Nature 215: 476-480.

Mather, K.
1953 The genetical structure of populations. Symposia of the Society for Experimental Biology 7: 66-95.

Montagu, A.
1965 The Human Revolution. New York: Bantam Books.

Parker, S.T. and K.R. Gibson
1979 A developmental model for the evolution of language and intelligence in early hominids. The Behavioral and Brain Sciences 2: 367-381.

Patterson, B., A.K. Behrensmeyer and D. Sill
1970 Geology and fauna of a new Pliocene locality in northwest Kenya. Nature 226: 918-921.

Patterson, B. and W.W. Howells
1967 Hominid humeral fragment from early Pleistocene of north western Kenya. Azania 2: 1-15.

Pilbeam, D.
1966 Notes on *Ramapithecus*, the earliest known hominid, and *Dryopithecus*. American Journal of Physical Anthropology, n.s. 25: 1-15.

1968 The earliest hominids. Nature 219: 1334-1338.

Pontifical Academy of Sciences Symposium
1982 Agreed Statement on Recent Advances in Our Knowledge of Primate (including Human) Evolution. (In press).

Rensch, R.A.
1959 Evolution above the Species Level. London: Methuen.

Reyment, R.A.
1975 Analysis of a generic level transition in Cretaceous ammonites. Evolution 28: 665-676.

Robinson, J.T.
1972 Early Hominid Posture and Locomotion. Chicago and London: University of Chicago Press.

Salzano, F.M.
1975 The Role of Natural Selection in Human Evolution. Amsterdam/Oxford: North-Holland Publishing Company.

Schmalhausen, I.I.
1949 Factors of Evolution: the Theory of Stabilizing Selection. Philadelphia: Blakiston.

Simons, E.L.
1961 The phyletic position of *Ramapithecus*. Yale Peabody Museum of Natural History Postilla 57: 9p.

1964 On the mandible of *Ramapithecus*. Proceedings of the National Academy of Sciences 51(3): 528-535.

1968 A source for dental comparison of *Ramapithecus* with *Australopithecus* and *Homo*. South African Journal of Science 64(2): 92-112.

Simons, E.L. and D. Pilbeam
1965 Preliminary revision of the Dryopithecinae (Pongidae, Anthropoidea). Folia Primatologica 3: 81-152.

Simpson, G.G.
1944 Tempo and Mode in Evolution. New York: Columbia University Press.

1953 The Major Features of Evolution. New York: Columbia University Press.

Snowdon, C.T. and J.A. French
1979 Ontogeny does not always recapitulate phylogeny. The Behavioral and Brain Sciences 2: 397-398.

Tobias, P.V.
1967 Olduvai Gorge, Vol. 2: The Cranium and Maxillary Dentition of *Australopithecus* (*Zinjanthropus*) *boisei*. Cambridge: University Press.

1968 The age of death among the australopithecines. Special Volume, The Anthropologist, University of Delhi: 23-28.

1970 Brain-size, grey matter and race — fact or fiction? American Journal of Physical Anthropology 32(1): 3-26.

1971a The Brain in Hominid Evolution. New York/London: Columbia University Press: 1-170.

1971b The distribution of cranial capacity values among living hominids. Proceedings III International Congress Primatology, Zurich, 1970. Vol. 1: 18-35.

1974a Aspects of pathology and death among early hominids. The Leech 44(3): 119-124.

1974b *Homo erectus*. Encyclopaedia Britannica (15th edn), vol. 8: 1030-1036.

1975a Long or short hominid phylogenies? Paleontological and molecular evidences. *In*: F.M. Salzano (ed), The Role of Natural Selection in Human Evolution, Chapter 6, Pp. 89-118. Amsterdam/Oxford: North Holland.

1975b Brain evolution in the Hominoidea. *In*: R.H. Tuttle (ed), Primate Functional Morphology and Evolution, Pp. 353-392. The Hague/Paris: Mouton.

1978 Primatology, paleoanthropology and reticulate evolution: concluding remarks. *In*: D.J. Chivers and K.A. Joysey (eds), Recent Advances in Primatology, Vol. 3, Evolution, Pp. 507-509. London/New York/San Francisco: Academic Press.

1980a "*Australopithecus afarensis*" and *A. africanus*: critique and an alternative hypothesis. Paleontologia Africana 23: 1-17.

1980b L'évolution du cerveau humain. La Recherche 11(109): 282-292.

1981a The evolution of the human brain, intellect and spirit. 1st Andrew Abbie Memorial Lecture, Pp. 1-70. Adelaide: University Press.

1981b The emergence of man in Africa and beyond. Philosophical Transactions, Royal Society 292: 43-66.

1982 Olduvai Gorge, Vol. 4, *Homo habilis*. (In press).

Vogel, E.
1975 Remarks on the reconstruction of the dental arcade of *Ramapithecus*. *In*: R.H. Tuttle (ed), Paleoanthropology, Morphology and Paleoecology, Pp. 87-98. The Hague/Paris: Mouton.

Von Koenigswald, G.H.R.
1972 Was ist *Ramapithecus*? Natur und Museum 102(5): 173-187.

1973 *Australopithecus*, *Meganthropus* and *Ramapithecus*. Journal of Human Evolution 2: 487-491.

White, T.D., D.C. Johanson and W.H. Kimbel
1981 *Australopithecus africanus*: its phyletic position reconsidered. South African Journal of Science 77: 445-470.

Wolpoff, M.H.
1971 Metric Trends in Hominid Dental Evolution. Case Western Reserve University Studies in Anthropology 2: 1-244.

Wynn, T.
1981 The intelligence of Oldowan hominids. Journal of Human Evolution 10: 529-541.

Question Period I

Cooke: There is one question that I would like to ask Dr. Tobias. He said very little about *Homo erectus* in Africa. *Homo erectus* is going to form the subject matter of our afternoon talk; he might just like to say a word or two about *Homo erectus* in Africa.

Tobias: I mentioned them only by name, Dr. Cooke. There are *Homo erectus* specimens from East Africa: a particularly beautiful specimen known as Olduvai hominid 9, another one, hominid 12, from Olduvai, with all the characteristic morphological hallmarks of a *Homo erectus*. There are others also from farther north. In northwest Africa, there is a cluster of fossil discoveries, from Algeria and Morocco which have been classified as *Homo erectus mauritanicus,* another sub-species. So that phase of humanity is represented. It's dubious whether we've got it in South Africa. There's a mandible from the Cave of Hearths, which is dated to over a hundred thousand years ago. It probably is not old enough, but it certainly has some morphological features reminiscent of *Homo erectus*. Then there are some problematical ones like what used to be called Rhodesian Man, the Broken Hill skull which the late Carleton Coon classified as *Homo erectus*, and others as *Homo sapiens*. It certainly has intermediate features, as does the Saldanha skull from 100 miles north of Capetown. So, scattered in a patchy way there are manifestations of *Homo erectus* in Africa .

Question: I actually have three questions, one of which goes back to the very beginning of the talk, and two which are concerned with more recent work on the South African material. The first of them concerns the discussions of the Pontifical Academy meetings in May 1982, and relates to what might be called the replacement of *Ramapithecus*. From my reading, there appears to be some indication that there are two other genera, normally referred to as *Dryopithecus* and *Sivapithecus*. I'd like to know whether any agreement was made as to a possible replacement — is the *Dryo-Siva* split still acceptable, and can it be related to the origin of hominids?

Tobias: As far as *Dryopithecus* is concerned, there certainly is agreement that it is pongid, i.e. a member of the ape family. There is an interesting new development now. Reassessing bigger samples of the Indian and African fossils, it has been suggested that, possibly for the wrong reasons, Louis Leakey was right, in suggesting that *Proconsul*, the early East African higher primate, should not be in the same genus as Asian *Dryopithecus*, and should be regarded as belonging to another family which Louis had proposed to call the *Proconsulidae*. So some "*Dryopithecus*" remains *Dryopithecus*, while some may be taken away. Some of the earlier Afro-Asian linkages which were proposed might indeed need to be broken up. Of *Ramapithecus* there is an African version and an Asian version. It was the late Ralph Von Koenigswald who considered the Asian *Ramapithecus* as hominid, and the African *Ramapithecus*, (which Louis Leakey had called *Kenyapithecus*), as something different. The new view is that it is *Sivapithecus* which seems closest of all to a common ancestor, that is a member of the common population, from which pongids and hominids diverged. That is the one that is now staking a claim to be closest to the common ancestral population. *Rama-* is out, *Dryo-* remains well and truly entrenched within the apes whether we regard the African and Asian forms as belonging to one or to two separate families.

Cooke: Just as an addendum, some important material has been found in China that I am sure Dr. Wu will be talking about, that also belongs to this *Ramapithecus*. May we have your second question?

Question: The other two, I think, are very closely related; one of them has to do with Taung. I was wondering whether there seems to be any agreement as to whether the very young dates that have been quoted for Taung, are in fact correct; I was also wondering in a much more general way whether you would comment on the fact that no further sites have in fact been discovered in South Africa since 1948.

Tobias: As far as Taung is concerned, it is still a very difficult problem. Professor Cooke said its dating is uncertain. Partridge, on the one hand, by one set of techniques, and Butzer, from Chicago, on the other hand, by another set of techniques, have both come up with a very young age which may be one and a half million years or less. If that is so, the problem is that we have no other example of *Australopithecus africanus*, as such surviving so late. This is a problem which isn't yet resolved. Some years ago, I stuck my neck out, and said that if it is really only one million years old, then it couldn't be the same thing as Sterkfontein and Makapansgat. Or at least it was doubtful whether it would have grown up to be a "Mr. Ples." It could well have to be considered as a possible youngster of the robust lineage, without our worrying about the name for a minute. That's another complication. We will have a Diamond Jubilee of Taung in early 1985 and I hope by that stage our total restudy of the Taung child and its dating will have been completed, and that we may be able to answer it then. I can't give a final answer on that one, at the moment.

Cooke: There certainly are a number of points of difference in the teeth of Taung from those of Sterkfontein and Makapansgat.

Tobias: Robert Broom pointed them out, and he was a suberb morphologist. Whether he was a good taxonomist is a different question altogether. But if he observed something, it was there. A number of those early observations have been confirmed recently. For example, there is a tuberculum sextum on the lower molar of Taung, differentiating it from Sterkfontein and Makapansgat. Whether such differences are enough to permit us to say it clearly belongs with *A. robustus*, and not with the Sterkfontein-Makapansgat fossils is still problematical. Brain casts and some facial features have suggested that it belongs with the gracile *A. africanus*. Only some dental features have supported the alternative possibility. However, it needs further work. I'm sorry to leave something dangling in midair. Yet it's strange that the first discovered specimen of all of them, found 58 years ago, is still an enigma in my opinion. We hope to regain access to the Taung site, and to do further field work and excavating there. The original site which has been buried under a mantle of lime dust many metres thick for decades, is, I hope, going to be removed and reopened, and it is just possible we may have some exciting news for the Diamond Jubilee.

Cooke: Are there any other questions?

Question: I am wondering about the evidence from an ecological and ethological perspective would require the need for an equivalent to *Ramapithecus* in terms of an edge of forest shift type of habitation which would necessarily be at a transition to an open-living kind of primate, the same way as Ngorongoro would be found in a more open veld-kind of environment and would conceivably have been bipedal already. Would that justify an earlier shift than the molecular evidence suggests?

Tobias: Yes, that's quite a tricky one. There are at least two different viewpoints on the paleoecology of *Ramapithecus*. There is the viewpoint that it was a creature living in a heavily wooded terrain, but it's been argued by others again, that a good case could be made for its having been in a more open savannah kind of environment. This has not been resolved between the different paleoecologists involved. As to the paleoclimatic shift, are you referring to late Pliocene drying up in Africa?

Questioner: No, I'm still back in the Miocene.

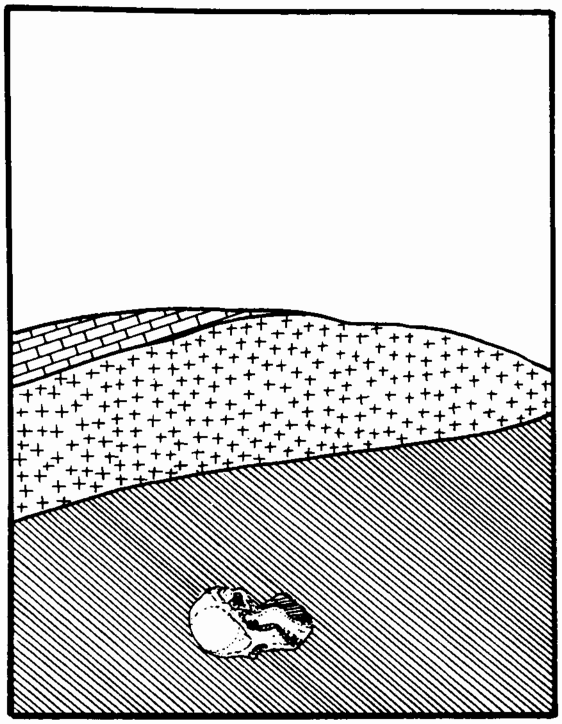
Tobias: You're still back in the Miocene, of course, if you are talking about *Ramapithecus*. I don't know whether it would affect the evidence of the biological relationships between the hominids and pongids to the extent that it would alter the divergence time. Their divergence time is based on pure biological evidence. Maybe the answer is that the ecological tolerance limits of early hominids and hominoids were very great and that it wasn't direct ecological determinism that generated that particular cladogenesis, which led to pongids and hominids. It would be very nice and tidy if good ecological paleoclimatic determinism was one of the key factors in effecting the split. I don't think there is enough evidence to justify such a claim, but I'd appreciate hearing Basil Cooke's view on that one.

Cooke: No, I think that we need a great deal more information put together about the environmental conditions at all the *Ramapithecus* sites: China, and Europe, perhaps Turkey, Africa... and then we may see whether there is any characteristic that they share in common. I think we can't answer your question, because we don't have the data. Are there any other questions?

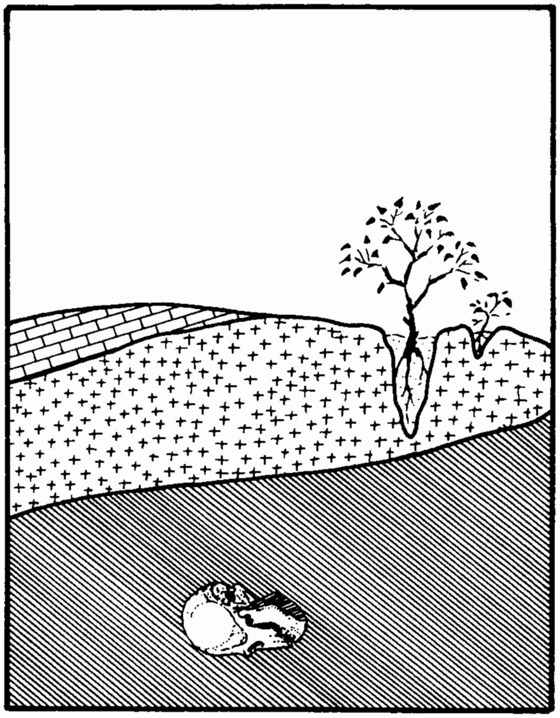
Question: I believe there were some tools found in conjunction with Australopithecines at the Hadar site. Can you comment on the extent of tool use among the Australopithecines and compare it with the usage of tools by *Homo habilis*?

Cooke: The question is that there are supposed to be tools found at Hadar; could we comment on tool usage by *Homo habilis* and *Australopithecus*? I think that I might just save Phillip a bit of breath on this one. The fact is, you have tools and you have fossils, and you have fossils of monkeys and pigs and elephants all together. When you have more than one hominid in a deposit, it's very difficult to decide which made the tools. So, I'll see whether Phillip has anything to add.

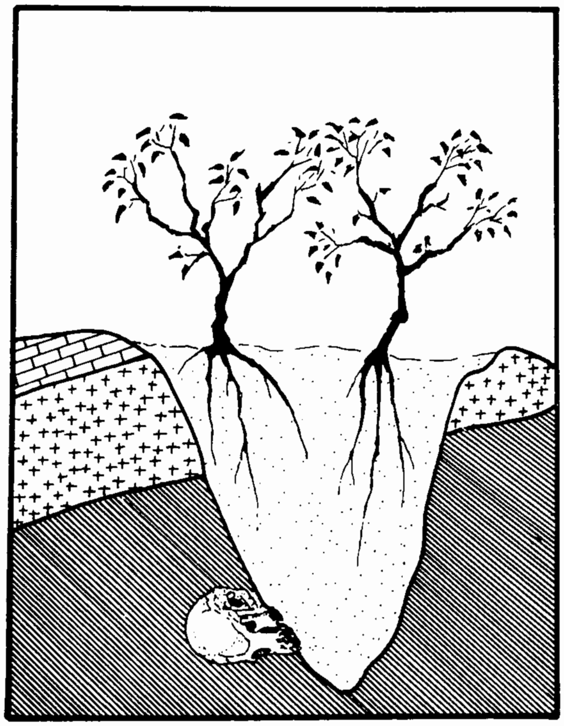
Tobias: The tools you speak of at Hadar go back to something like two and a half million years. There are a few very dubious fragments for which a date of nearer to three million years has been claimed. But there are just a very very few, and Coppens has referred to them recently. But they are not certain evidence that the hominid of three million years ago was a stone tool maker. Coming up a little more recently, we have good confirmed tool-making, and I'm poaching on Glynn Isaac's preserve here, from about 2.3 million years onward. Wherever it occurs, whatever other hominid may be present, there is at least *Homo habilis* present as well. Mary Leakey's meticulous analysis of Olduvai has shown pretty convincingly that although we've got two hominids side by side, the big robust *A. boisei* and the little petite *H. habilis*, it is



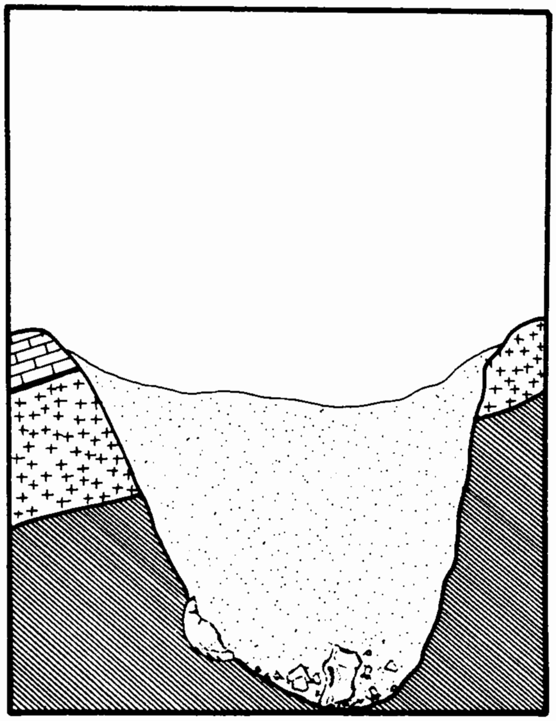
The cranium and jaw are embedded in Member 5. The overlying Member 6 and a part of the original dolomite roof of the cave are shown also.



The de-roofed breccia of Member 6 becomes decalcified around the spreading roots of vegetation. As a result sinkholes filled with soft deposits are formed.



A sinkhole has become very large and the process of decalcification has intersected the skull.



Broken fragments of the cranium and teeth are now in the soft filling, while a large portion of the vault of the same skull is still in the solid, calcified wall of the sinkhole.

(From Tobias, P.V.: "Hominid Evolution in Africa").

with *H. Habilis* that the tool-making seems to be associated. She has at least 6 good living floor associations there, if not more. And we have associations of that kind now also in Sterkfontein, member 5.

What about tool-making in *Australopithecus*? What about Professor Dart's old theory of the osteodontokeratic culture, the bone, tooth and horn culture? Dart suggested in the fifties (indeed he suggested even in the twenties, but didn't develop it until the fifties), that there might have been usage of the bones which formed the food, the prey, as he regarded it, of *Australopithecus*. The recent remarkable study by Bob Brain, published by the University of Chicago press, has shown that almost all of the bones that are broken, damaged, or unequally worn, from Makapansgat, and remember, they run to hundreds of thousands, can be explained by other means than hominid activity. Carnivores, whether leopard, or a slightly bigger version, a sabre-tooth, or hyena or predatory birds, porcupines and smaller rodents, all of these can, at the hands of Brain, now be identified from the nature of damage that those species inflict on bones. The assemblages are now identifiable. He has formed the conclusion that if *Australopithecus* of that time had anything to do with those hundreds of thousands of bits of bone, it was a negligible element in the total spectrum of other causal factors which were operating on those bones. To add all this up, it looks as though — one says it with a certain amount of nostalgic sadness, because Dart was my old teacher — it looks as though the osteodontokeratic culture is a beautiful theory that has been slain by some very ugly facts. I don't think it has stood the test of time. Well, what did *Australopithecus* do with his hands? If he didn't make those bone tools, and if those aren't bone tools, the possibility is that like the chimps and gorillas, he used perishables. Jane Goodall's chimpanzees in Tanzania used leaves, twigs, bark, branches. It's quite possible that perishables might have been used for the implemental activities, such as they were, of *Australopithecus*. We have found fossil wood at Sterkfontein last month.

Cooke: It's a good thing that the carnivores lived in a throw-away society.

Early Man in Indonesia: The "Defossilization" of Human Fossils

TEUKU JACOB
Gadjah Mada University
YOGYAKARTA, Indonesia

Abstract: Fossil remains from Java have been discovered in three main periods of research at seven sites in three Pleistocene beds. They consist of fragments from three regions of the skeleton, and constitute three genera representing three stages of hominid evolution.

Important characteristics, as revealed by the actual remains, concern the size and shape of the skull, the teeth and the lower limb. Secondary interpretation pertains to the size and shape of the body, while tertiary and subsequent interpretations touch upon the behaviour, culture and environment, with progressively less precision and agreement among students of fossil man.

With regard to the antiquity of the fossils, there is as much argument as agreement. The best dates (by K Ar) were obtained by Curtis (1.9 million years to 600,000 years ago), but there are several claims of younger ages for differing reasons.

Phylogenetic affinities are considered in the light of new discoveries and with a flexible scheme. The latest finds described include a cranial endocast and a calotte from Sangiran.

Résumé: Des restes fossilisés venant de trois gisements datant du Pleistocène ont été découverts à Java lors de trois périodes de recherche parmi sept sites. Ces ossements fossilisés proviennent de trois régions du squelette et représentent trois genres, ou trois étapes dans l'évolution de l'hominide.

Les détails que nous révèlent ces fossiles portent sur les dimensions et la forme du crâne, sur la dentition, ainsi que sur les membres inférieurs. L'interprétation secondaire de certaines charactéristiques nous renseigne sur les dimensions et sur la forme du corps. L'interprétation tertiare et subséquente se rapporte au comportement, à la culture, et à l'environnement. A cause du manque de précision dans ce domaine, cette dernière catégorie d'interprétation est cependant sujette à certaines divergences d'opinions parmi les étudiants de fossiles humains.

Il y a aussi controverse en ce qui concerne l'âge des fossiles. Les dates les plus sûres (de 1.9 million à 600,000 ans) ont été obtenues par Curtis. D'autres dates moins avancées ont cependant aussi été suggérées.

De nouvelles découvertes, tels un moulage endocrânien (endocast) et une calotte provenant de Sangiran, ont remis en question certaines affinités phylogénétiques. La reconsidération de ces affinités à l'intérieur d'un schéma plus flexible fera donc partie de cette étude.

*Keywords: **Homo erectus***, **Java, cannibalism, hominid fossils, Indonesia.**

THE FINDS

Three periods of activity can be recognized in the history of Indonesian paleoanthropology since the days of the discovery of *Pithecanthropus* by Dubois until the present:

1. 1889-1899-the Wajak, Kedungbrubus and Trinil discoveries, comprising skulls, jaws, femora and vertebrae were made in this decade;
2. 1931-1941-the Ngandong, Perning and Sangiran discoveries comprising skulls, jaws, teeth, and tibiae were made in this decade;
3. 1952-1982-in these three decades more discoveries were made at Sangiran, Ngandong and Trinil, and also at Sambungmachan; they comprise skulls, endocasts, jaws, teeth, tibiae, femora and pelvic bones.

As noted above, seven sites are known:

1. Wajak: skulls, jaws, vertebrae and a femur, of Late Pleistocene age.
2. Kedungbrubus: a mandible, of Middle Pleistocene age
3. Trinil: skulls and femora, of Middle and Late Pleistocene age.
4. Ngandong: skulls, tibiae and a pelvic bone, of Middle Pleistocene age.
5. Perning: a skull, of Early Pleistocene age.
6. Sangiran: skulls, endocasts, jaws, teeth, femora and tibiae, of Early, Middle and Late Pleistocene age.
7. Sambungmachan: a skull, of Early/Middle Pleistocene age.

All the fossils belong to only three skeletal groups, i.e.:

1. the cranium: mainly calvaria, especially the occipital and parietal bones,
2. the jaws: mainly mandibles, and teeth, especially molar and anterior teeth.
3. the limbs: mainly lower limb bones, especially femora.

Vertebrae were found only at Wajak, namely the cervical vertebrae.

Of the calavarial bones we have mainly the following portions:

a) occipital bone: the occipital plane;
b) parietal bone: the parietal eminence;
c) frontal bone: the supraorbital torus;
d) temporal bone: the mastoid process.

The facial bones are usually represented by:

a) mandibular fragments, mainly the anterior portions and teeth, especially molars, no ramus;
b) maxillary fragments, especially the premolar region;
c) zygomatic bones.

In addition, we have natural endocranial casts, basilar portions of the occipital bones, sphenoid bones and nasal bones. The best preserved calvaria is Ng 7; and the most complete specimens are S 17, S 34, the Ng 8 tibia, and the T 3 femur.

All finds were secondarily deposited by volcanic and river actions, and therefore:

1. no complete skeleton or skeletal regions or functional complex are available for study;
2. mandibles were never found associated with the corresponding cranium or maxilla;
3. most skulls have damaged bases;
4. most long bones are shafts or their fragments.

It is important to note here that all Ngandong finds were discovered in excavations. At Sangiran for the first time we found a hominid fossil (femoral fragments) associated with animal fossils and a stone tool during excavations in 1978.

THEIR TRAITS

Characteristics of *Pithecanthropus* are by now widely known. Almost all reported cranial features are the results of three morphological trait complexes, namely:

1. the small endocranial volume;
2. the robust splanchnocranium;
3. the slight deflection of the cranial base (Jacob 1980).

To reconstruct the living body and population of *Pithecanthropus*, we should "defossilize" the frozen fossil fragments. The ultimate goal of defossilization is to reconstruct from bone fragments a human group, interacting in the ecosystem, constantly moving and changing in time and space. To do this, various stages have to be considered in the right order. From a bone fragment we try to reconstruct the complete bone, and from this we move to related bones, the skeletal part, the surrounding soft parts, the body part, the whole body, the individual, and finally the group. It is obvious that the farther we go, the more vulnerable we will be to errors of extrapolation, particularly if we pursue derived traits, such as the size and shape and the functions of body parts, body build and physiognomy, ontogeny, and behaviour.

Between the death of an individual and the laboratory study of his fossilized remains, many events have taken place which affect the nature of body parts. We have to trace back step by step all these events in making the reconstruction which, of course, is only partially possible. Intra-vitam violence which occurred just before death and which led to death cannot be distinguished from post-mortem violence occurring just after death. Transport influenced the nature and completeness of body parts. Pre-fossilization events might be confused with post-fossilization events. Damage could occur during transport from the site of primary deposition to the site of secondary deposition, before fossilization took place. This period is crucial for understanding the process of fossilization; however, many factors are involved, and its mechanisms and outside intervention are unknown, either in general or in individual cases.

Fossilization, just like death, is not an instantaneous process; it might even occur at more than one site. Then, transport could occur again after fossilization and before discovery. And discovery itself is not necessarily a single event taking place in a short time. Finally, transportation of the fossil after its discovery might cause other damage, besides traumata occurring during the recovery of the fossil and during packing. Afterwards, the fossil might suffer during handling or a *force majeur*, such as war, when it could be destroyed or lost.

Fossilization itself is a rare occurrence, and only a small portion of the fossilized bones ever reached scientific institutions. Hence, the fossil material studied is usually small, non-random and incomplete. Nevertheless, we have to "defossilize" the fossil material beyond their strict anatomical description so that those rare remains may assume some meaning.

On several occasions, the author has attempted to reveal different degrees of derived traits of the Indonesian fossil hominids. New finds support earlier observations, including the data presented by the new endocast; only S 27 conveys cranial features not found in other pithecanthropine material.

THEIR ANTIQUITY

Fortunately, K Ar dating is applicable to the volcanic deposits in central Java. The antiquity of most Indonesian hominid fossils has a time range from around 2 million years to 0.1 mya. However, the Wajak fossils and likewise the later fossils from Sangiran and Trinil (occipital bones, femora) have an antiquity of 0.04 to 0.01 (estimated) mya.

The first age determination of the site of the Mojokerto discovery at Perning was reported as 1.9 ± 0.5 mya. Younger dates of the Puchangan beds have subsequently been reported, but unpublished new dates by different groups of workers tend to support the older dates.

Dates related to several Sangiran finds range from 1.1 to 0.7 mya. Younger dates have also been reported on several occasions, but again unpublished support for the older dates has been suggested.

Chronometric dates by various methods would be very useful in resolving the problem of antiquity of Indonesian hominids, or at least in decreasing the arguments and disagreements stemming from contradictory results. In fact, younger or older dates *per se* are not that important; what is significant for us is their consequent interpretation.

It should be noted that Java, at least part of it, was part of the Sunda subcontinent during the glacial periods with consequent low sea levels, but studies in paleogeography in this region are not sufficient to be useful in elucidating man's early history. Nevertheless, at several periods during the Pleistocene, people were able to walk from mainland Asia to Java.

THEIR AFFINITY

Indonesian hominid finds have been compared and associated with those from Beijing, Lantian, Neandertal, Olduvai, Arago, and Cohuna-Kow Swamp. It seems to me that the association with the *erectus* group is more convincing than to the *sapiens*, Neanderthal, or australopithecine groups.

Wajak, of course, is undoubtedly *Homo sapiens*, and belongs to the same group and episode as Niah (Borneo) and Tabon (Palawan). The later fossils from Sangiran and Trinil might also belong to this same group.

In establishing affinity, the antiquity and paleogeography have to be taken into account, in addition to the morphological trait complexes. As has been widely recognized, an anthropological trait on a fossil fragment cannot be regarded as fact in isolation because it has its evolutionary history, its functional, comparative and genetic aspects, as well as sexual dimorphism and ontogeny. Time and space are *sine qua non* factors in evolution.

S 27 is very interesting because it presents some features not found in other Indonesian pithecanthropines. Among others, it shows well-marked parietal crests, and bulging canine alveoli. On the other hand, the calvarial bones are thick and the curved supraorbital tori are separated above the glabella. This fossil is the oldest among the Sangiran fossils from the Puchangan beds.

THEIR INTERPRETATION

After summarizing the fossil finds, the background of their discoveries, the biostratigraphy, the morphological traits, the antiquity and the affinity, we naturally come to their interpretation. Identification, we know, involves mechanisms of the diagnostic process at different levels of analysis, as in any other discipline, and in paleobiology it also involves all levels of the living system. As we go up to the higher levels of the system, we leave the secure realm of anatomical description of available body parts, and the increasing uncertainties make us more susceptible to errors of judgment.

As we all are aware, the theory of human evolution underwent evolution, too. All four evolutionary factors have their role to play. Mutation, in the form of new facts and finds, starts a series of new interpretations which then are subjected to selection: only those which conform to the existing rules and paradigms survive and multiply. Now and then a major mutation triggers quantum evolution which results in megaevolution of a theory. In general. the evolution of hypotheses and theories involve microevolution, minor changes taking place from generation to generation of experts. Microevolution could occur due to a breakthrough in science or a very important find. Students immediately exploit the new adaptive zone, and adaptive radiation develops and characterizes this explosive stage.

Gene flow from other disciplines acts constantly, and genetic drift occasionally has the opportunity to play its part. Orthogenesis rarely occurs in the evolution of an evolutionary theory, and the principle of irreversability is usually also valid; the direction of evolution could be similar to the previous one, but the pathway is different.

As in biological evolution, parallelism, convergence and divergence are also observed in the evolution of an evolutionary theory. And extinction is not infrequent: a theory reaches a dead end, develops into a new theory or hybridizes with another. Cladogenesis is more often encountered than anagenesis. The rate of evolution depends on the stage and the pattern of evolution; if it takes the form of arrested evolution, the rate is extremely slow.

The taxonomy of theories of human evolution is very complex, although two families are generally recognized, *i.e.*, lumpers and splitters. True lumpers do not believe this, of course, because there is continuous gradation between extreme lumpers and extreme splitters.

There is no doubt whatsoever that the evolutionary theory continues to evolve. The hypodigm, in the form of paleoanthropological hardware, namely the fossil material, grows constantly with the increasing number of discoveries in more areas of the world. The paradigm, in the form of paleoanthropological software, changes with scientific progress and the philosophical climate. Similarly, technology exerts its influence on the paradigm, such as the computer in taxonomy, electron microscopy in identification, chronometric dating, etc. Therefore, a relaxed mental attitude in lieu of fanaticism is a prerequisite in the unending study of human evolution.

SUMMARY

After discussing the discovery sites, and the nature of the finds, primary morphological traits directly observed on the fossils were grouped into three trait complexes: small endocranial volume, robust splanchnocranium and slight deflection of the cranial base. But in order to reconstruct human life of the past, we have to "defossilize" the frozen fossils. We have to recognize at least that important events had taken place between the death of an individual and the recovery of his fossilized remains, or better, their arrival in the laboratory.

The antiquity and the affinity of Indonesian hominid fossils have been discussed. After touching on interpretation, a reflection is given on how one might view the evolution of evolutionary interpretation.

ACKNOWLEDGEMENTS

Friedrich Braches and Richard Shutler checked the spelling of place names in this article and Prof. Jacob's discussion sections (editor).

REFERENCES

Colbert, E.H.O.
1969 Some paleontological principles significant in human evolution. *In*: W.W. Howells (ed.), Early Man in the Far East, Pp. 103-147. Anthropological Publications, Oosterhout N.B.

Dart, R.A.
1959 Adventures with the Missing Link. New York: The Viking Press.

Dubois, E.
1894 *Pithecanthropus erectus*, eine menschenahnliche Ubergangsform aus Java. Batavia: Landesdruckerei.

Genet-Varcin, E.
1979 Les Hommes Fossiles. Paris: Societe Nouvelle des Editions Boubee.

Howells, W.W.
1980 *Homo erectus* — Who, when and where: A survey. Yearbook of Physical Anthropology 23:1-23.

Jacob, T.
1970 Penjelidikan paleoanthropologi di Indonesia. Berkala Ilmu Kedokteran. Gadjah Mada 2(2): 135-144.

1972 The problem of head-hunting and brain-eating among Pleistocene men in Indonesia. Archaeology and Physical Anthropology in Oceania 7(2): 81-91.

1975a Morphology and paleoecology of early man in Java. *In*: R.H. Tuttle (ed.), Paleoanthropology: Morphology and Paleoecology, Pp. 311-325. The Hague: Mouton.

1975b The pithecanthropines of Indonesia. Societe d'Anthropologie de Paris, Bulletins et Memoires, series 13(13): 243-256.

1978 The puzzle of Solo man. *In:* G.-J. Barstra (ed.), Modern Quaternary Research in Southeast Asia, vol. 4: 31-40. Rotterdam: Balkema.

1979 Hominine evolution in South East Asia. Archaeology and Physical Anthropology in Oceania 14(1):1-10.

1980 *Meganthropus*, *Pithecanthropus* and *Homo sapiens* in Indonesia: Evidence and problems. Paris, Coll. Int. CNRS: Les Processus de l'Hominisation.

1981a Solo man and Peking man. *In*: B.A. Sigmon and J.S. Cybulski (eds.), *Homo erectus*: Papers in Honor of Davidson Black, Pp.87-104. Toronto: University of Toronto Press.

1981b *Pithecanthropus* dari Trinil: Tafsirannya selama 90 tahun. Seminar in Anthropology. Yogyakarta.

1981c Methodologi penelitian dan analysis paleoanthropologi. Rap. Eval. Met. Penel. Arkeol., Yogyakarta.

Jacob, T. and D. Kadar
1981 A new pithecanthropine cranial endocast S 34 from the Sangiran dome area, Central Java. Publ. Geol. Res. Devel. Centre, Paleont. Ser. (1): 1-7.

Koenigswald, G.H.R. von
1962 Speurtocht in de Prehistorie. Utrecht: Prisma-Boeken.

Konigsson, L-K (ed.)
1980 Current Argument on Early Man. Oxford: Pergamon Press.

Kuhn, T.
1972 Scientific paradigms. *In*: B. Barnes (ed.), Sociology of Science. Pp. 80-104. Harmondsworth, Middlesex: Penguin.

Leakey, L.S.B., J. Prost, and S. Prost (eds.)
1971 Adam, or Ape: A Sourcebook of Discoveries About Early Man. Cambridge: Schenkman.

Mayr, E.
1976 Evolution and the Diversity of Life. Cambridge: Belknap Press of Harvard University Press.

Rensch, B.
1972 Neuere Probleme der Abstammungslehre. 3. Aufl. Stuttgart: Ferdinand Enke Verlag.

Simpson, G.G.
1961 Principles of Animal Taxonomy. New York: Columbia University Press.

Soejono, R.P. (ed.)
1982 Sejarah Nasional Indonesia I. Jaman Prasejarah di Indonesia, ed. 3. Departemen Pendidikan dan Kebudayaan, Jakarta.

Sutjipto, F.A. (ed.)
1976 Sejarah Nasional Indonesia IV. Indonesia Dalam Abad 18 dan 19, ed. 2. Departemen Pendidikan dan Kebudayaan, Jakarta.

Villiers, J.
1965 Sudostasien vor der Kolonialzeit. Frankfurt am Main: Fischer Bucherei.

Washburn, S.L.
1973 Human evolution: Science or game? Yearbook of Physical Anthropology 17:67

Wellington, J.S.
1975 Some aspects of the social history of medical education and medical care in Indonesia. Hasil Pert. Nas. Anthrop. PAAI, pp. 58-65.

Wolpoff, M.H.
1980 Paleoanthropology. New York: Alfred A. Knopf.

Ziegler, B.
1975 Einfuhrung in die Palaobiologie 1. Allgemeine Palaeontologie. Stuttgart: Schweizerbart'sche Verlagsbuchhandlung.

THE CENTER FOR THE STUDY OF EARLY MAN

The Center for the Study of Early Man was established in 1981 as part of the Institute for Quaternary Studies at the University of Maine–Orono, under the direction of Robson Bonnichsen. The principal objective of the Center is to improve scientific and public understanding of the earliest human occupation of the Americas. Long term goals of the Center include the coordination and stimulation of early man research, publication of these findings, and the development of educational programs for a wide cross-section of people.

The *PEOPLING OF THE AMERICAS SERIES*, published by the Center for the Study of Early Man, is designed to focus interdisciplinary attention on the problem of human occupation of the Americas before 10,000 years before present. Alan L. Bryan and Ruth Gruhn are editors of the series. The first two volumes will be published in 1983. Anticipated volumes for the series include:

UNDERSTANDING STONE TOOLS: A COGNITIVE APPROACH
David E. Young and Robson Bonnichsen

NEW EVIDENCE FOR THE PLEISTOCENE PEOPLING OF THE AMERICAS
Contributions in English, Spanish and Portuguese with estensive English abstracts
Alan L. Bryan (Ed.)

ENVIRONMENT AND EXTINCTIONS: MAN IN THE LATE GLACIAL NORTH AMERICA
James I. Mead and David J. Meltzer (Eds.)

ANIMAL REMAINS FROM ARCHAEOLOGICAL SITES
D. Gentry Steele and B. Miles Gilbert (Eds.)

ARCHAEOLOGICAL SEDIMENTS IN CONTEXT
Julie K. Stein and William R. Farrand (Eds.)

—ORDER NOW FOR A PRE-PUBLICATION DISCOUNT—

Please send me a copy of UNDERSTANDING STONE TOOLS: A COGNITIVE APPROACH by Young and Bonnichsen ($24.00, soft cover)

Please keep me informed about the publication of other volumes in the Peopling of the Americas Series

Send to: NAME ______________________________
INSTITUTION ______________________________
ADDRESS ______________________________
____
____

A Money Order Check Purchase Order is enclosed for $. [Subtract 10% for professional discount and an additional 10% for orders mailed before August 31, 1983. Add $3.00 book rate postage and handling in the U.S. and Canada and $13.00 overseas air mail book postage and handling.]

Send to: *Beech Hill Enterprises, Inc.*, P.O. box 229, Mount Desert, Maine 04660

Question Period II

Question: Could you elaborate on the type of environment in which fossils occur?

Jacob: Between death and fossilization many processes take place. Fossilization is not an instantaneous transformation. Pre-fossilization processes are numerous. Transport may have occurred. In Indonesia most of the finds are from secondary deposits. Fossils were deposited by the stream action of rivers or lahar flows. The Sangiran site, for instance, was at some time a shallow sea, later a Pleistocene lake and is now located in the delta of a large river. At Ngandong, different from Sangiran and other sites, fossils have been found in river terraces. Mostly broken shafts of long bones were found, whereas unbroken bones are extremely scarce. Intact long bones, however, are reported from deposits of volcanic origin by various researchers. Some remains are found fossilized in lahar flows without any damage to the bones if they had not been carried over too long a distance by the lahar flow. Intact fossils have been found at Sangiran and quite a few other places. Fossil skulls of water buffalos were discovered intact as the result of the conditions of the deposition in central and east Java.

Cooke: It seems to be quite an analogy between this and the Omo situation, where we have river systems coming out of the volcanic highlands of Ethiopia, transporting eroding material in the river, causing a great deal of damage. Then the material floated into the flood plains by the chance storms, and were buried, causing a great deal of damage. This is very much unlike the situation in the East Turkana region where we have lake shore environments, very sluggish rivers, and the possibility of specimens being buried almost immediately after exposure, with very little transport. So there is a difference. It seems to me, that it's a little unfortunate that Java belongs to this highly transported regime, which has frustrated the Omo researchers for so long. For the benefit of those of you who are not familiar with geology, you may not be familiar with the term lahar flow. It is not a lava flow; it's the kind of event that took place with the eruption of Mount Saint Helen's, where a volcanic eruption, as a consequence, produces a tremendous upsurge of moisture into the atmosphere. This leads to condensation, the development of thunder clouds, and intense rain. The rain then produces mud flows which carry enormous volumes of material down the flanks of the volcano into the plains below. This is a lahar flow. It's not really lava, but it contains volcanic chunks and anything that happens to be in the way including living animals, which will be dumped down and buried, which would account for your water buffalo skulls. These lahar flows are worth a great deal of further investigation, even though one is looking for a needle in a haystack.

Question: I'd like to ask what percentage of the fossils are being found in a secondary deposition and in the context of being in a secondary depostion, how are they being dated?

Jacob: Yes, that is a very good question. The dating was done with pumice samples taken from layers which extend over a large area and can be traced throughout the site. Sampling was done, in other words, from a continuous pumice layer. If the pumice layer was not a continuous one but only a very localized deposit, the layer was not used for dating purposes. At some sites, such as Sangiran, we could locate three layers of pumice: one at the layer of the fossils, one below that layer and another one above it. At Mojokerto the sample was obtained 1.5 m below the fossil layer. In the case of Mojokerto the entire bed is around 200 m thick. For the dates of Sangiran 10 and Sangiran 17, there are at least two layers where we could take pumice samples. But for Ngandong no dates are available since no suitable samples were found. One date obtained — not associated with human fossils — from Lower Pleistocene beds was 1.8 mya. Other series of dates from the Upper Pliocene Kalibeng formation up to the Notopuro formation are forthcoming.

Cooke: It is very good to know that some new dating is coming out of these pumices because they always look promising and frustrating. I hope that you are also doing some fission track dating to tie in with the K-Ar because we have been misled by pure potassium/argon dates. Does that answer your question? What percentage of secondary deposition as opposed to primary deposition?

Jacob: Most of them are secondary. In some cases the remains seem not to have been carried far away, perhaps not more than one kilometre in our estimation. But in many other cases, they were carried a few hundred kilometres from the supposedly original site.

Cooke: To follow up this question, are there any samples of specimens that were fossilized and mineralized before transportation and burial, that is rederivation of fossils? Are there any cases where the transported specimen is already fossilized?

Jacob: Oh, yes. In some cases, we have cranial endocasts with two distinct kinds of fossilization, not only of the matrix but also in the distribution of the matrix on the specimen. We think these must be successive fossilization processes. Although the division is not a well marked straight line in the endocast, one type is external to the other in such a way that one can really separate them.

Question: I just wanted to question Dr. Jacob on the dating of the Mojokerto remains. Was the original site marked? I was wondering how you managed to relocate it in order to take the pumice sample from below it?

Cooke: The question is, the dating of the Mojokerto site, was it possible to relocate the site exactly enough to get samples which give reliable dates for that particular deposit?

Jacob: According to our geologists, yes. With the help of contour maps of von Koenigswald and others it is possible to track down the fossiliferous layers. At Mojokerto the animal fossils are not as widely scattered as at Sangiran. Molluscs are surface fossils. At this site we could easily detect the thin layer with land animal fossils. An indication of the exact spot in centimetres or decimetres is possible, but considering that the whole bed is about 200 metres thick, an approximation of 1.5 m below the fossil layer should not create much error. This is corroborated by other Pucangan dates from Sangiran. It is of course the best to use the bones for dating. Dating from the matrix is not always satisfactory.

Question: Thank you. Just another question, please. Is there a difference in the dating between the bones and the matrix?

Jacob: Of course there is an error factor, but it seems that the correct date is closer to 1.9 than to 1.5 mya. Other dates obtained later are closer to 1.9 mya.

Cooke: Thank you. You had another question?

Question: Yes sir. Do you believe the so-called Meganthropus specimens are closer to *Australopithecus* or *Homo erectus*?

Cooke: You are opening a new can of worms.

Jacob: Yes, if you open a can of worms, it is impossible to put them back in the same can. A few will remain outside. But this is very interesting because of the finds I showed you: a distorted skull with a thick supra-orbital torus, big molars and massive maxilla, which may belong to what is called *Meganthropus*. The calvarial bones are not thin but comparable to those of other *erectus* specimens. The characteristics which differ from those of other *Homo erectus* skulls are: the bilateral crest on the parietal bones, the nasal aperture, the shape of the maxilla and the mastoid region. In a secondary deposit we could, of course, not expect to find the mandible associated with this maxilla and we had to match other *Meganthropus* mandibles with the maxilla. The layers where this find was made were deeper than the earlier finds such as the "dubious" mandible and Sangiran 9 and others. If *Meganthropus* was in Java, this must be his skull. But we are continuing the study of this specimen, because it is quite distorted, especially in the occipital region.

Question: So, you would tend to associate it more with *Pithecanthropus erectus* than with *Australopithecus*.

Jacob: Yes, although I hope to find thin parts of the skull. We are not entirely satisfied with the condition of the skull bones which suggest a closer relationship with *erectus* than *Australopithecus*.

Question: Thank you very much.

Cooke: That sounds like the sort of provocative question we might raise for the panel tomorrow morning. Phillip, will you say something about it tomorrow?

Question: Dr. Jacob, I'd like to ask if you would address the problem of the comparative lack of facial skeletons found in the Java specimens, and do you believe it lends any credence to the theory of cannibalism being practised by these creatures?

Cooke: How about a faceless race of man?

Jacob: Yes, why are they all losing face? Big problem. I think that when people eat one or two other human beings in an emergency siuation we cannot speak about the occurrence as cannibalism. This happens many times. But if a group eats human beings routinely, then this is cannibalism. There are three reasons why routine cannibalism is impossible. One reason is population dynamics. It is impossible to live on your own species. No species has existed that lives on its own members. It is impossible that self eats selves. It is impossible to have a community eating members of its own group. Because the group cannot survive on that basis. I have made some calculations and found that the group would last for only eighteen months. It is also not a very economic way of getting protein. Another reason against routine cannibalism is that the number of humans was only very small relative to the population of large animals. These people would try not to disturb the cohesiveness of their community. They would rather hunt other protein-carrying animals in their environment. Perhaps we could digress somewhat longer on the interesting subject of cannibalism. Firstly, population dynamics seem to speak against routine cannibalism. Secondly, ecosystem energetics provide an argument against cannibalism. There is no food chain or ecological pyramid if the chain is broken by a species eating its own kind. That would under usual circumstances create a real change in the ecosystem. There would be no interaction between species and it becomes impossible to survive. The way the system of energy flow is set up contradicts the occurrence of cannibalism in all species. Thirdly, the evidence used to demonstrate the presence of routine cannibalism is not conclusive. Take for instance the absence of the base of the face of prehistoric man. Why do we only find calvarial bones? Simply because shape, morphology and the even thickness of these bones seem to make them more suitable to be fossilized. On the other hand, bones of irregular shape, with many orifices and fissures and not of the same thickness are more likely to be destroyed, particularly in transportation. These are, in my opinion, the reasons why "faceless" hominids have been found in this area and also elsewhere. Fragments of the cranial base are not readily recognizable as important finds, as for instance the occipital condyle. When it is found on its own it is hard to distinguish whether it is a hominid condyle or the condyle of a small animal. We tried to piece together the basal portion of the occipital out of eleven small fragments to get a good specimen of the occipital bones. I think that in such cases we should not let ourselves be carried away by sensationalism, but should try to use logic.

Cooke: This is borne out very much by the Omo discoveries, where again, the easily destroyed bones are missing, and they are largely faceless. As far as cannibalism is concerned, I've always wondered why when New Guinea is so close, why Dr. Jacob has this resistance to the idea of cannibalism. But as I also feel, if one looks at primitive societies, cannibalism is not a routine way of getting a living, but on the other hand, as Flanders and Swan said in their song, "Reluctant Cannibal," "If the great Ju-ju had not meant us to eat people, he wouldn't have made us of meat." They don't always ignore an available supply.

Question: I'd like to ask Dr. Jacob whether the studies of the animal fossils, whether any of these bones show any evidence of work, were cuts made by stone tools, or any other evidence of tool making, besides that stone you mentioned?

Jacob: There are only one or two pieces of bone so far which we think might have been used or modified by man. This is not very convincing, at least not convincing enough for others. We do hope that one day we will get better evidence if such evidence is available at all. Early man could have used perishable plant materials instead of bone. Hypotheses have been made that they might have used bamboo if bamboo was available. We do not know this yet. Perhaps if lots of plants were available they would not look for rocks a distance away to make useful tools for the exploitation of their environment. So far we do not have any convincing evidence of the use of bone for tools from our excavations.

Cooke: Are there any other questions?

Question: It seems to me that in the work that's being done in Africa, there is a lot of emphasis on the importance of meat, and meat sharing, and other aspects of behaviour which no doubt Glynn Isaac will be getting into tomorrow. And, some of the most interesting work has been done on cut marks on bone, not bone being used as tools, but evidence of tool use and its effects upon bone.

Jacob: No, we have not done that kind of study yet, so if anybody is interested we would welcome the initiative. Thank you.

Question: I was wondering if you would discuss the taxonomic status and dating of Solo Man. I have heard some fairly early dates in the last few years, and Solo Man was previously considered as a separate species, but also in the rank of Neanderthal Man. Would you discuss that one?

Jacob: Well, it depends how far we want to go with the differentiation. If we compare Ngandong finds with other *erectus* finds, Ngandong is closer to the *erectus* group than to the *Homo sapiens* group. That is why I do not include Ngandong man among the *Homo sapiens*. The age of Ngandong? There is one date, not a very good one, of 300,000 years. But other dates from Notopuro seem to be in the same range and we know that the Notopuro formation could be related to some of the terraces of the Solo river at Ngandong and surroundings. Consequently in my estimation, Ngandong's age is between 100,000 and 300,000 years. If a line is drawn between the Late Pleistocene and the Middle Pleistocene at 130,000 years, then of course Ngandong belongs to the Middle Pleistocene groups. It depends where we put the boundary. I think that Ngandong finds are at least 100,000 years old and should be placed in the Upper Pleistocene. But the age is perhaps more likely somewhere between 100,000 and 300,000 years.

Cooke: A propos, I seem to remember a thesis being published recently which suggests that the Ngandong skulls are very similar to the Sangiran, and fall within the same morphological group. Do you remember this paper?

Jacob: Yes, I think that the differences are only in size and that in general the shape is closer to *erectus* than to *sapiens*. Comparing Ngandong skulls with some finds of the *erectus* group from Java and with the Peking material — studied in this case from the cast — I think that Ngandong in many aspects is closer to Choukoutien than to the Javanese *erectus*. In general grouping, Ngandong evidently belongs to the other Javanese *erectus* fossils and is different from the later *sapiens* groups like Wajak.

First Panel Discussion

Cooke: One of the issues that came up yesterday that seems to me to warrant further discussion is the rejection by Phillip Tobias and his cohorts of *Ramapithecus* from its rather pleasantly established position in time and space as a possible member of the hominid line. Then we heard a rather schizophrenic attack on the *Ramapithecus/Sivapithecus* problem which we didn't resolve. I think we might get a little more resolution of the *Sivapithecus/Ramapithecus* problem from these two aspects. Phillip, would you like to leap to the defense?

Tobias: Well, *Ramapithecus* had been something of an enigma because the people who believed that it could be regarded as a hominid based on its morphology had very incomplete material to go by. One of the crucial points was, for instance, the reduction of the canine tooth. The canine tooth as you have seen is very large in pongids; it's small in hominids. One of the marks of the members of the family of man is to have a small-sized canine whose tip projects barely at all beyond the crown surfaces of the adjacent teeth. There are exceptions! When you have only one or two of these very ancient *Ramapithecus* fossils such as the ones from the Punjab it is very hard to be sure if one is dealing with a truly reduced canine. It was a difference in morphological judgment as to just how reduced must a canine be before we'd regard it as a hominid sort of canine that led to the early differences of opinion. Pilbeam and Simons, formerly both of Yale, were the two main supporters of the idea that *Ramapithecus* was a hominid. At that stage there were no other kinds of evidence to suggest that a more recent origin of the hominids might have been nearer the truth. The dates of these *Ramapithecus* fossils were between about 12 million and 15 to 18 mya, if Louis Leakey's finds in East Africa belong to the same kind. When the molecular evidence increasingly pointed to a more recent origin of the hominids, people started looking at the morphology of *Ramapithecus* much more critically than previously. In fact there were those like John Robinson who from the beginning had said unequivocally that, on the anatomy of those *Ramapithecus* fossils, there wasn't anything on the basis of which to declare them hominid. He wasn't alone in that. People like Wolpoff, Eckhardt, and others had questioned the hominid attribution of *Ramapithecus*. Of those who had studied the originals, there were about six or seven strong supporters on the one hand, and four or five strong opponents. Presently, it becomes irreconcilable with the molecular data to have so ancient an origin of the hominids. The molecules show 99% of what we consist of is shared in common with chimpanzees. Re-examining the the morphology of *Ramapithecus* in the light of this newer information, Pilbeam and Elwyn Simons, both present with me at that Vatican meeting in May 1982, declared that they now abandon their former strong view in favour of *Ramapithecus* being a hominid. They drew attention to the fact that its morphology really was equivocal and one could not place it unequivocally among the hominids. More complete material from China and elsewhere now supports a more orangoid affinity for those early *Ramapithecus* fossils. I think that's enough to kick off with, Basil.

Cooke: Dr. Wu would you like to say anything further?

Wu: I am in agreement. So far as the material in our hands goes, the differences between *Sivapithecus* and *Ramapithecus*, as I have said today, are more like sexual differences instead of generic differences. So, I believe, from a morphological point of view, that *Ramapithecus* seems more likely to be the ancestor of orang instead of hominid.

Holloway: I'd like to make a comment, first about the molecular evidence; I refuse, absolutely refuse to be bullied by this... It's all well and nice to talk about 99% homogeneity of DNA sequences and the example was given recently of this argument between the palaeontologist and the molecular biologist and it was in the Sunday section of the *New York Times* magazine, in which the author stated that the difference between ourselves and chimpanzees was something of the order of one codon per thousand pages. So that if we talked about the difference between ourselves and chimpanzees for example, it would just be a matter of flipping through the pages and every thousand pages or so you could see this difference in the codon specifying an amino acid and thereby specifiying a different polypeptide. I think this is rubbish. What you probably do is skim a few hundred pages perhaps a thousand, and then you get intensely interested in about 2 pages of changes.

Probably not at a structural DNA level at all, but at RNA levels or satellite RNA, which is regulatory, and then you might go on for a couple of thousand pages and find nothing different. In other words, there are sets of punctuations which we don't know a thing about and so we're really sampling the molecular evidence. We don't know what we're talking about in terms of the actual genetic changes, and what morphological characteristics they effected, or when they effected them. So that's my comment on molecularism.

Dr. Wu, I wanted to ask a question. I got the impression, when you first showed a picture of what you call *Ramapithecus* that the degree of sectorialization of the lower third (or first) premolar, seemed to me to be less than that of *Sivapithecus*.

Wu: Yes, that's right.

Holloway: Then that is a very crucial morphological difference between the two.

Wu: No, it's the same thing as different sexual characteristics.

Holloway: I see. The degree of sectorialization you explain as simply due to sexual dimorphism.

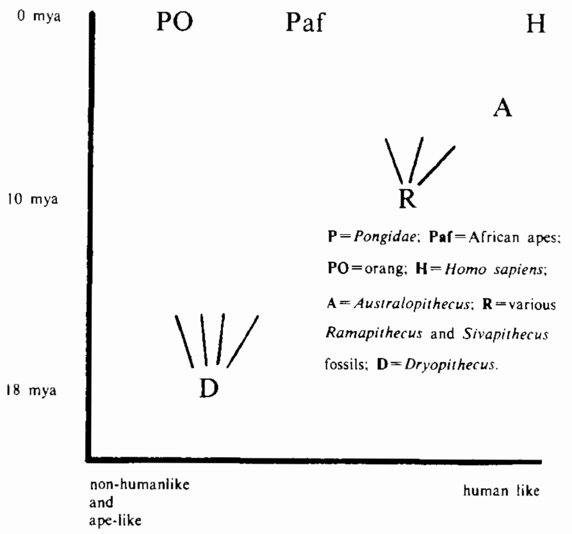
Cooke: In other words, the same kinds of differences observed between male and female orangutan.

Isaac: Let me take up comment on behalf of a group which is not here — I refer to the scientists who do comparative biochemistry as a source of information about evolution. These include close colleagues at Berkeley such as Vincent Sarich and Allan Wilson. They would, I think have been shaken by Phillip Tobias' suggestion yesterday that a grand new synthesis had been arrived at in the Vatican in 1982. The biochemists started to advocate that kind of position way back in 1966. I think at this point it would be fair for us scholars of the stratified record to eat humble pie. The odds are now overwhelmingly in favour of the biochemist's having been right and the paleontologists being wrong. Listening to talks, one could get the impression now that the paleontological camp had been divided on this issue — but it really wasn't. The great majority of paleontologists refused to accept either the relevance or the validity of the molecular evidence. We owe the molecular scientists thanks for their assistance in this aspect of our studies.

Tobias: What was new about the recent development from 1975 onwards, and what I described as the consummation at the Vatican this year (1982), was that all sides were represented there, the molecular biologists, the chromosome merchants, the paleontologists, including those who were the *Ramapithecus* supporters; and for the first time everybody agreed that the data indicated by the molecular evidence, that those directions, did seem seriously to be nearer the truth, than the original interpretations from the fossils. So it was a new synthesis, I truly believe that.

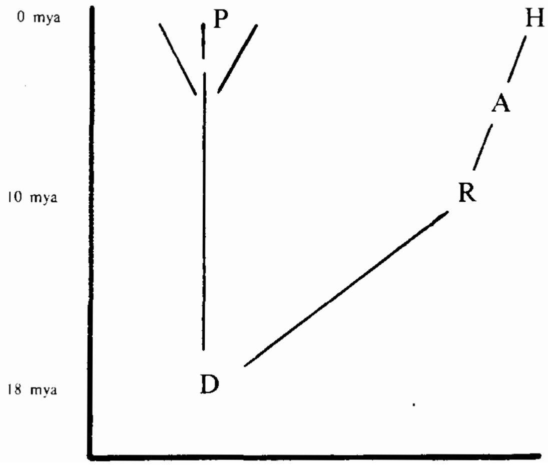
Isaac: There's another point that I might make, and that's that the material attributed to *Ramapithecus* comes from a wide variety of geographic localities and across a lot of time. I think it would perhaps be unwise to hastily assume that what is true of one set of "*Ramapithecus*" fossils in one place is necessarily true for them all. And if we're learning, as one hopes we are, in paleoanthropology, to work with multiple alternative hypotheses, it still might be too early to make a decision about how the fossils interrelate. Let me put on the board for discussion this diagram which draws on David Pilbeam's writings and ideas.

Frame A

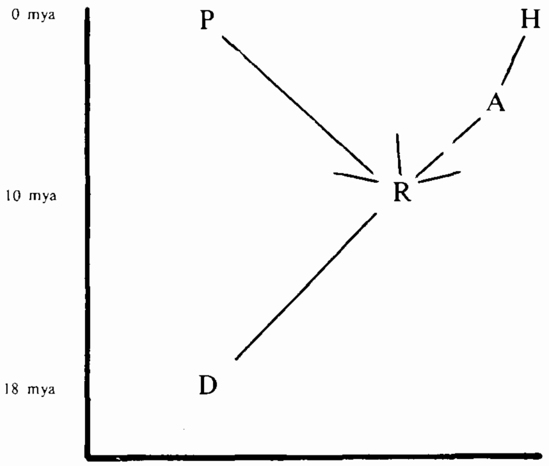


This first frame shows the empirical data, namely distinctive fossil forms arranged in relation to a scale of human-likeness and arranged in time. The subsequent frames show different hypotheses about phylogenetic relationships.

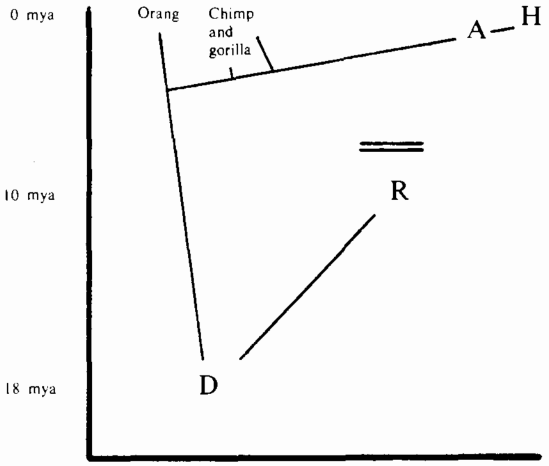
Frame B



Frame C



Frame D



Frame B is incompatible with the molecular evidence and can effectively be eliminated. Frames C and D remain variable alternative interpretations, between which we cannot yet decide. Note that we have no fossil record for African ape evolution during the past 5 to 10 million years. Getting this record is almost as important as getting more human ancestry fossils.

Tobias: Actually, I've got a slide here that is Pilbeam's latest chart and it might be quite interesting to show it at this stage. (Slide projected).

Tobias: This on your left was the sort of picture that, as Glynn Isaac was demonstrating, was the agreed wisdom of a couple of years ago. On your right is the very much less cocksure pattern which Pilbeam published last year. And you see from that the *Dryopith* group down at the bottom and earlier in time. Up on your top left the pongid group and its base is left uncertain. On your top right is the hominid group and its base is left uncertain. And hovering in a kind of twilight zone in the middle he's created or suggested a group called the *Ramapithecidae*, in which he puts *Ramapithecus*, *Sivapithecus*, *Gigantopithecus* as a member of a kind of twilight group. He has left it open in his most recent publication how to join up those different lines, and where indeed to trace the exact lineage. The hominid line is certainly going back now, including the newest discoveries by Desmond Clark, to a point where it is very close paleontologically to pongids. It looks as though, within the next couple of years, we'll be able to make a more confident diagram than that top right hand one. But that on the right has replaced this previous attempt on the left. That's Pilbeam 1981.

Cooke: Thank you both, Glynn Isaac and Phillip Tobias, for these last contributions and Ralph Holloway for his defence of the anti-molecularists. One of the delightful things about paleoanthropology and in fact about paleontology in general is how easy it is to draw beautiful diagrams when you have very little evidence; how very much more difficult it becomes when the evidence begins to accumulate. So let's hope that we'll reach a kind of a point at which we have enough evidence to start again and re-examine this question. In the meantime, it looks as if *Ramapithecus* is put on the shelf and we're not quite sure if *Ramapithecus* is the mate of *Sivapithecus* or just a permanent contemporary like the chimpanzee and gorilla. I personally have some reservations about the molecular ideas, because it seems to me that there are some anatomical characteristics in man which require a lot of evolution, and one of these is the complexity of the human foot. The other is the extraordinary changes in the pelvis and in the upright stature and in the hand. And these things seem to me, from what evidence we now have, thanks to things like Lucy, and the beautiful fossil imprints that we have in the lavas in Laetoli that at 3.5 mya we already had a very good human foot, that we already had upright walking, already had very good hands, and it seems to me that the molecular biologists are not giving enough time for the transition from the ape structure, or the basic monkey structure even, to the hominid structure. I'd like to throw this at the panel to see whether they'd like to take it up. I love being shot down.

Holloway: I'll follow up on it. I'm not anti-molecular at all. It's just that I don't want to be bullied by it. I think a great deal of hope and promise of a true synthesis between the kinds of observations of phenotypic characteristics and actual molecular events really lie in molecular biology. And that bridge that's going to be gapped is a very exciting one of physiology, and it's going to come back where it's been lost for decades. One of the things that I'm absolutely compulsive about is units. What are we talking about if we can't define units of variation? As you'll see from my talk, if we don't know what's varying and we don't know the adaptive value of the morphological characteristic that's varying we really have nothing to talk about in terms of selection. And the units that we're talking about in paleoanthroplogy are so gross that you have to keep them in mind. We're talking about brain size and I'll have more to say about that of course. What is brain size? And bipedal locomotion? As if this were a unit in its own way, as if you could put it into some morphological axis along the abscissa. This is nonsense. This is a tremendously complex process, and it doesn't just involve the bony and muscular shifts and reorganizations but it damn well has to involve the nervous system too. You have to get those changes taking place. It doesn't occur in a behavioural vacuum either. Bipedal locomotion gets used in some sort of adaptive strategy that's behavioural. We keep talking about these things and the recent diagram on the board has this lovely nebulous zone of *Ramapithecus/Sivapithecus.* I wish we could talk more about real straight-forward units like the sectorial P-3 which on my question can be explained as a simple sexual dimorphic characteristic. But I think that is the point that is quite right. We've got to start identifying very carefully units of variation within these highly complex morphological complexes and start talking about them. Then the molecular evidence starts coming in. It's all well and good to talk about how close our blood groups are between ourselves and gorillas and what not, but you know if you start examining certain kinds of satellite DNA the gorilla turns out to be closest to the human. It's just extraordinary what you can do with the molecular evidence. I'm not anti-molecular but I want to see it in a proper perspective.

Cooke: Dr. Tobias, I'm sure you're itching to get back into the act.

Tobias: A couple of my slides yesterday attempted to show the very point that Ralph's just been making and that is that the attainment of upright posture and bipedal gait is an extraordinarily complex process which, as I pointed out, involves adjustments, anatomical and functional, in every part of the axis of the body from the base of the skull, to the tip of the toes. An important concept to mention here, which may help us a little and also help perhaps our chairman's point, is the concept of mosaic evolution. We must abandon the idea that all parts of our body were hominizing *pari passu*, that they were all going forward in line like a common wave front towards ultimate manhood. There is abundant evidence now that some parts evolved rapidly, earlier on, and then slowed up. Other parts evolved rapidly later on, having been virtually dormant in the earlier stages. We did not hominize in a completely homogeneous wavefront pattern, but rather in what is called a mosaic evolutionary pattern. Now, although Mary Leakey's delightful footprints from Laetoli show clearcut evidence that there was a bipedal higher primate, walking around there at that stage, where we do have bones of the earlier hominids' feet, it's been shown by a colleague in London that one can recognize incomplete degrees of hominization of the foot. The foot was mosaically out of step, if I can be forgiven the term, with the knee, and the knee joint was mosaically out of step with the hip-joint and the pelvis. So, not everything became like modern man at the same pace. One could draw a graph of the rate of hominization of different features. I mentioned yesterday that the brain seemed to obtain its final enlargement, its aggrandizement, belatedly as one of the later events in the processes of hominization. There isn't "a process" of hominization. I think that that concept is a help in our thinking. You could come upright as recently as 4 million years ago, and then still undergo further adjustments. Dash it all, we are not yet fully adapted to our uprightness. We still get hernias, and prolapses, slipped discs and backaches, and postural headaches, and the most widespread pandemic condition of modern humanity, malposture, — all of these things are errors of uprightness. They are the ills of uprightness. We have only been doing it for four or five million years, and we haven't quite got used to the idea even yet!

Holloway: I think you forgot about flat feet.

Tobias: Precisely!

Holloway: I think some comment ought to be made about this over-all approach which faults our present condition on the basis of "incomplete" past adaptation. Natural selection doesn't give a damn if our feet are flat, our disks are slipped, we herniate, or have strokes, heart attacks, etc., etc., provided we at least duplicate our genes on the average of twice during our reproductive lives. Given the maladies afflicting mankind, where can one draw the line? Using Tobias' reasoning, we would have to conclude that our entire anatomy and physiological functioning is imperfectly adapted, including our brains. Furthermore, I'm sure one could extend this line of reasoning to many other species. Up to a third of Adolph Schultz's gibbons showed evidence of injuries, many from falls. Should we conclude that brachiation among the *Hylobatidae* was an imperfect adaption for which extant gibbons are paying the price?

Cooke: Glynn Isaac has a comment to make.

Isaac: I was interested in Basil's challenge, that something as complex as the adoption of bipedal gait would have to have taken a long time. If we had a larger panel, some colleagues would be present who would flatly disagree and say that intermediate stages in moving upright, that is a tripedalism, is inherently improbable. And the march of mankind, the kind that greets us at the door out there, with stooping forms that gradually become more vertical, this is inherently improbable. It is most likely that if the transition to upright gait was going to be achieved, it would have to happen fairly rapidly. The reason why we explore the record of the past is to find out which of these two hypotheses is correct. We cannot wisely deduce it *a priori.*

Cooke: Well, the answer is we have a lot of problems. We seem to have solved some, we have a lot of evidence, but what we really need is to get into that time gap between 4 and 8 mya. So, the more money we can get from foundations the better. Ralph

Holloway, I don't know if he is asking for money, or what...

Holloway: That is a fine idea, I was thinking of it. Actually, I wanted to direct another question to Wu if I can...

Cooke: A question for Dr. Wu, yes.

Holloway: Dr. Wu, you mentioned yesterday that many of the *Ramapithecus-Sivapithecus* pieces are very fragmentary. May I ask whether there are any squamal portions of occipital bone that could render endocranial casts?

Wu: The bones are quite distorted.

Holloway: I asked the question because these portions, endocranially, are going to be of very great importance in trying to decipher the evolutionary relationships between fossil and extant pongids, and in trying to determine which morphological characteristics are primitive or advanced. It is a pity to learn that the fragments are too distorted for any analyses. Let me give just one example. The Hadar *A. afarensis* materials suggest the presence of a marginal or accessory sinus traversing the lateral margin of the foramen magnum. As Tobias has shown, it appears on the OH 5 robust specimen. In fact, it appears on SK 1585, SK 849, KNM-ER 732 and 407, all female robust Australopithecines. It doesn't appear in any chimp or gorilla or orangutan endocasts I've examined. It doesn't appear in early *Homo*, nor in gracile *Australopithecus*. This is one reason I have very great trouble placing any *A. africanus* bridge between *A. afarensis* and *A. robustus*, or *boisei*. I am very hopeful that the Chinese fragments might eventually shed some light on this mystery. Furthermore, the position of the lunate sulcus is terribly important in trying to understand brain organization, and we must soon establish, once and for all, whether or not early pongids had the pattern either retained in present *Pan, Pongo,* and *Hylobates*, or whether it is a recently acquired pattern.

Cooke: The question relates to the possibility of getting endocranial casts from the Chinese *Ramapithecus-Sivapithecus* material. Unfortunately, there is too much distortion. So, I guess we will have to send Dr. Wu back to the field to get something better. I would like to direct one question, from the audience to Dr. Jacob. This concerns the age of the Mojokerto child's skull, which has been queried in a recent publication in a series on the archaeological prehistory of South Asia. Do you have any comment to make?

Jacob: I think that the date of the Perning child or Mojokerto child is not as late as that published in later publications. Because, we have some more dates from Sangiran, from the Pucangan beds and the Kalibeng beds, which is the upper Pliocene, which confirm the older date. So we have dates of 2.9 mya from the upper Pliocene, and 1.5 plus or minus 2.5 mya for the middle mark of the Pucangan formation. So for the moment at least, I will believe the older dates of this rather than the younger dates as established by other groups.

Cooke: Do you take the 1.9 or the 1.5 mya?

Jacob: I think from the element test made on Sambungmacan and Sangiran, the dates would be closer to 1.8 than 1.5 mya.

Cooke: Thank you. That settles that question. Another question which came from a number of people is, what do we really know about the transition from *Australopithecus* to *Homo*? Anyone care to tackle that one? It looks as though we are woefully ignorant. So, it's a question of whether we have lateral rapid divergence, or continuous evolution. This comes back to the question Phillip was talking about yesterday. Another question which came from several people was the interrelationship between tools and *Homo*. Who made the tools, *Homo*, or *Australopithecus*, and why do we think that? Perhaps Glynn Isaac would like to anticipate his afternoon talk, at least for a few words.

Isaac: Basically all that one can usefully say is that tools do not appear in the record until the time range where we have evidence of the earliest forms with somewhat expanded, relative and absolute, brain cases, that is, fossils that are candidates for being the oldest known members of the genus *Homo*. So, since we see ourselves as lineal descendents of those chaps, and since we think tools were a smart innovation to have got into, we are emotionally inclined to attribute early tool making to the genus *Homo*. However, there is nothing in the logic of the situation to keep *Australopithecus* from having made tools. And as far as I know, there is no firm archaeological evidence to refute the hypothesis that both forms made tools, or, though I regard it as extremely unlikely, that the robust Australopithecine made tools and *Homo* didn't. Let me just for a moment, hop back to the previous question about the transition from *Australopithecus* to *Homo*. In the period four to two mya, in any one locality, we have only one form of hominid. This view is debatable, but many people would claim that it is the case. There may have been between the many regions of Africa, trivially different forms of *Australopithecus*, different regional species, but in any case, in any one region, there seems to be only one. Now, at the two million year mark, the whole record now becomes far more complex. Both in South Africa and in East Africa, many sedimentary deposits now start to contain two forms, one of which appears to undergo a trend to a large body size, the other of which undergoes an opposite trend, involving tooth reduction and brain enlargement. There is a distinct possiblility that one of the mechanisms that was involved here is the breaking down of geographic barriers, and competition between specifically distinct forms of *Australopithecus*, which undergo what is commonly called niche partitioning and character displacement. In the competitive situation which developed, one of them adopted an adaptive strategy which involved tools, perhaps increased carrying and meat-eating, while the other shifted to exaggerated Australopithecine characteristics, eventually, of course, becoming extinct.

Cooke: This is, in fact, one of the questions that I was handed, that is what is the basis for the three phase evolutionary concept of gradualism, punctualism and reticulation? I think, as Prof. Tobias said yesterday, this is an example of where we have punctuation. In a very short period we have divergence of a single stock into two stocks, and thereafter, we have in the one stock, the process of gradual and progressive evolution. I am also interested to see that Glynn Isaac is a left-handed *Homo* man. Do you have anything to add to that, Tobias?

Tobias: Well, this critical point, the one that I call explosive evolution, and which seems to have been about 2.3 million years ago, does mark the emergence of certain things in the hominid for the first time. And this may bear on the question: we see for the first time at this point here, the evidence of stone material culture emerging. We don't know if there was material culture earlier, we have not good evidence of it down here; there might have been a material culture based on perishables that haven't been fossilized, as I said yesterday. Yet here we see it expressed in imperishables, stone and very clear-cut defined patterns. We also see at this point, and Ralph, I presume will be coming to this in his paper, the onset of a rather remarkable degree of positively allometric enlargement of the brain, the brain enlarging far more rapidly than any change in body size would require or indicate. At the same time we see a curious trend of teeth becoming diminished in a particular fashion. It is rather interesting that here, and after, one finds African teeth and Asian teeth diminishing in different ways. The teeth in Africa, *Homo habilis*, leading on to *erectus*, become attenuated, instead of showing the tremendous width of Australopithecine teeth; the buccolingual diameter becomes appreciably reduced, especially in the premolars and first molar; it's less marked in the second and third molars. These are permanent teeth. And so the teeth become attenuated, and if I took an index of the length and breadth of the tooth, there is an appreciable change in its shape. Curiously enough, in Asia, when we pick up measurable teeth soon afterwards, one finds the overall reduction in size, but it is in length of tooth, not in the breadth. It is interesting and almost irresistible to inquire,in the light of what Dr. Wu said yesterday, about the early appearance of Mongoloid features, that if you reduced the teeth, in their lengthwise diameter, this is conducive to, or tied up with facial flattening, a feature of Mongoloid humanity. If you keep the teeth long, but reduce them transversely, this is in keeping with the more protruding, or prognathic jaw mechanisms characteristic of African humanity. It looks as though, that as long ago as this period, part of the basis of two of the major features differentiating living humanity, facial flattening or facial protrusion, may be evident. Getting back to the question, from this interesting sidelight, it seems as though dental reduction, jaw reduction, some change in the relationship between upper and lower teeth, which leads to a different pattern of occlusion, brain enlargement, I personally believe the appearance of Wernicke's area, supplementing Broca's area, as evidenced on the endocasts, connoting the cerebral basis of speech, and the tools, all make their appearance at that time. Those are the three most critical features marking the initial debouchment of *Homo*. ...If you take a point 40 million years ago and today, you could get an average rate of change. And the molecular biologists found that the rate of change in the lineage of horses, and the rates of change in the lineage of apes and men all worked out at approximately the same figure. It was all very unacceptable. But, with modification of some of their assumptions, but mainly, by supplementing their approach with other approaches, the basis has become much firmer. We no longer base it on a simple albumen clock. Since the cracking of the genetic code, to use a time honoured phrase, they are now able to do sequencing by electrofluoretic methods, sequencing of the proteins of man, chimp, gorilla, and everything else that lives, and they are able also to do D.N.A. sequencing. Each of these is a totally independent and different approach, D.N.A. sequencing, protein sequencing, and immunological distance. These three widely differing approaches all yield the same kind of results. It is this which has led to my being, to a degree, converted. I'm not hell bent in favour of the approach, I've accepted some aspects of its conclusions, but the concurrence of these three different approaches has led to its gaining much greater credibility. The chromosome data have come in, at the hands of cytogeneticists, using very refined techniques of banding of chromosomes and also using hybridisation studies. This has yielded a series of dividing points between apes and men, between African and Asian apes, orangutan and the African hominids, and there is some reasonable correlation between the cytogenetical and the molecular inferences. That is the kind of approach that our colleagues are using. It is this multiplicity of approaches converging on a reasonably common story of close interrelatedness between man and chimp, and man and gorilla, that has led to my conversion, or partial conversion, if you like.

Hominid Fossils From China and Their Bearing on Human Evolution

WU RUKANG (Woo Ju-Kang)
Institute of Vertebrate Paleontology and Paleoanthropology
Academia Sinica, P.O. Box 643
BEIJING (28) People's Republic of China

Abstract: A general review of hominoid fossils found from China in recent years is presented in chronological sequence: *Ramapithecus* and *Sivapithecus*, *Homo erectus*, early *Homo sapiens*, and late *Homo sapiens*. Their bearing on human evolution is illustrated.

Résumé: La présente est une revue chronologique des fossiles hominiens découverts en Chine ces dernières années, de *Ramapithecus* et *Sivapithecus*, *Homo erectus*, à l'*Homo sapiens* primitif ainsi que l'*Homo sapiens* moderne. Leur portée sur l'évolution humaine est aussi démontrée.

Keywords: **Hominid fossils, China, Ramapithecus, Sivapithecus.**

INTRODUCTION

China has been well-known for its famous Peking Man discovery. In recent years, many important finds have been made in the field of paleoanthropology, especially the skulls of *Ramapithecus* and *Sivapithecus* from Lufeng, Yunnan Province, the *Homo erectus* skull from Hexian County, Anhui Province, and the early *Homo sapiens* skull from Dali county, Shaanxi Province. All the finds will be summarized in chronological order.

RAMAPITHECUS AND *SIVAPITHECUS*

On December 1, 1980 a fairly well preserved skull of *Ramapithecus* was found from Shihuiba, Lufeng County, Yunnan Province. At that time, it was the first such skull found in the world. It attracted great attention from different circles.

Shihuiba is about 9 km to the north of Lufeng County and is situated on the south slope of the Miaoshanpo Hill. The fossil site in late Miocene beds was first found in 1975. Since then it has been excavated every year. Lots of fossil apes and other associated fossil animals were unearthed. Up to the present, we have recovered five fairly complete or incomplete skulls (Figures 1-3) and skull parts of *Ramapithecus* and *Sivapithecus* (Figures 4, 5), more than forty pieces of jaw bone fragments (Figures 6, 7)and more than 1000 teeth of both types. Also found were other animal fossils, including *Scaptochirus sp., Ictitherium gaudryi, Sivaonyx bathygnathus, Eomellivora sp., Hipparion cf. nagriensis, Tapirus sp., Lophochoerus sp., Dorcabune sp., Dorcatherium minus, Moschus cf primaevus*, etc. Fossil primates other than hominoids were also uncovered, including specimens of lorisids and hylobatids. All the materials are now being studied in detail.

Ramapithecus is traditionally believed to be the earliest known hominid, although there are reasons to doubt this classification. Preliminary studies show that the skulls of *Ramapithecus* and *Sivapithecus* have many features related to the orang-utan.

HOMO ERECTUS

Yuanmou Homo erectus

The Yuanmou *Homo erectus* was found by geologists northwest of Danawu Village, Yuanmou County, Yunnan Province on May 1, 1965. The fossils include the upper central incisors of the same individual. The lingual sides are shovel-shaped with a marked basal tubercle. Excavations of the site were carried out in 1967, 1971, 1973, and 1975. Many mammalian fossils, including *Equus yunnanensis, Muntiacus nanus, Canis yuanmoensis* were uncovered. In 1973, three quartz scrapers of medium size (42-48mm long) on thick square quartz flakes were unearthed (*Atlas of Primitive Man in China 1980:6*) The site was dated by the paleomagnetic method to be 1,700,000 mya. Recently, some authors believe that it is less than one million years old.

Figure 1. Superior view of cranium of *Ramapithecus* III from Lufeng County, Yunnan.

Figure 2. Basal view of cranium of *Ramapithecus* III from Lufeng County, Yunnan.

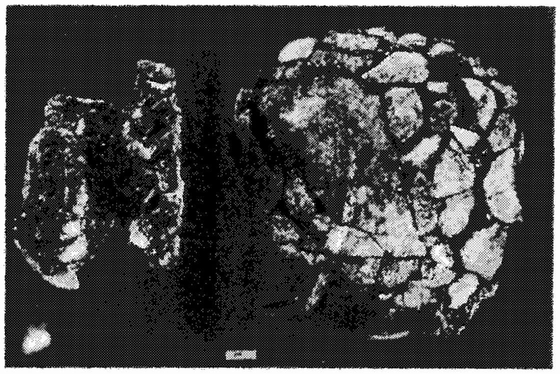


Figure 3. Superior aspect of cranium of *Ramapithecus* III from Lufeng County, Yunnan.

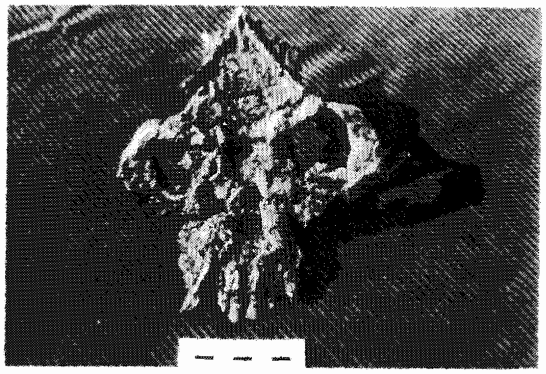


Figure 4. Frontal view of cranium of *Sivapithecus* from Lufeng County, Yunnan.

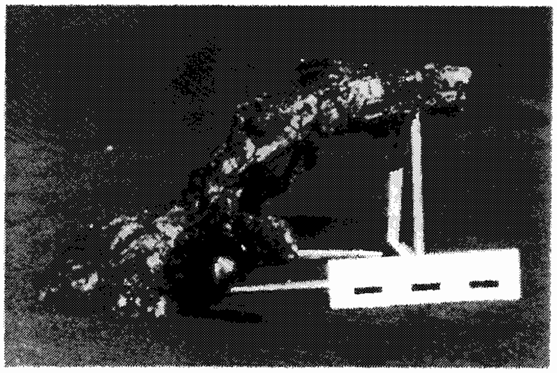


Figure 5. Lateral view of cranium of *Sivapithecus* from Lufeng County, Yunnan.

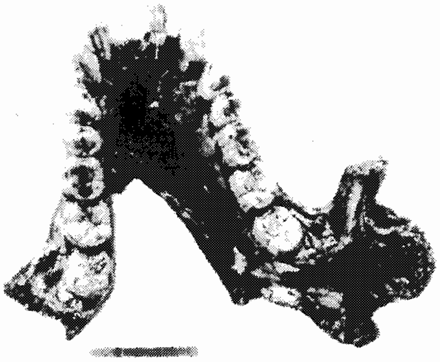


Figure 6. Occlusal view of mandible of *Ramapithecus* from Lufeng County, Yunnan.

Figure 7. Occlusal view of mandible of *Sivapithecus* from Lufeng County, Yunnan.

Lantian Homo erectus

Homo erectus fossils from Lantian include a mandible found at Chenjiawo Village, Lantian C County, Shaanxi Province in 1963 and a partial skull (Figure 8) and parts of these facial bones found in 1964 at Gongwangling in the same county. These specimens are morphologically more primitive than that of Peking Man. They were dated to be 0.7 mya. A few thick and heavy pointed chopping tools ("proto-handaxes") and scrapers (ibid:13) were found nearby.

Large numbers of mammalian fossils were found associated with the hominids, including *Megantereon lantianensis, Sinomegaceros konwanlinensis, Nestoritherium sinense, Ailuropa melanoleuca fovealis, Stegodon orientalis, Ursus cf. etruscus, Megamacaca lantianensis*, etc.

Figure 8. Reconstructed skull of *Homo erectus* from Lantian.

Zhoukoudian Homo erectus

The world famous *Homo erectus* site at Zhoukoudian, located 48 kilometres southwest of Beijing, was first found in 1921. From 1927, systematic excavations were made, and in 1929, the first skullcap of Peking Man was found. The excavation was stopped by the outbreak of the Sino-Japanese war in 1937. After an interruption of 12 years, excavations resumed in 1949 when New China was founded. Unfortunately, all the hominid fossils found before had been lost during the war. Beginning in 1949, new fossils of Peking Man have been found, including parts of a skull (Figure 9), a nearly complete mandible (Figure 10), isolated teeth and fragments of limb bones, in addition to a large amount of animal fossils and stone implements (Figure 11). In 1978 we started a comprehensive project to study this cave applying the method of horizontal archaeology in excavation. A monograph presenting the results of this study has been compiled and is now in press.

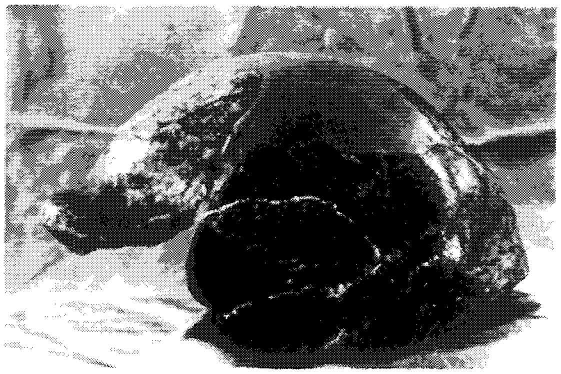


Figure 9. Skull cap of *Homo erectus* from Zhoukoudian Locality I (Peking Man Cave).

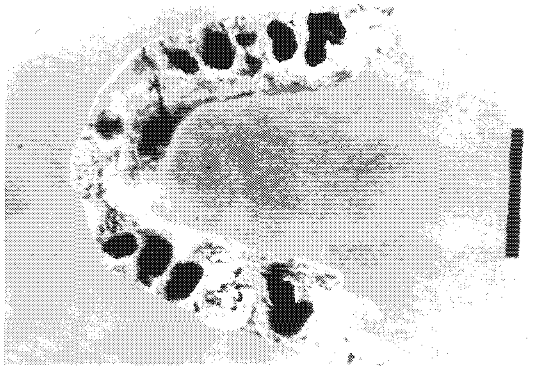


Figure 10. Mandible of *Homo erectus* from Zhoukoudian Locality I (Peking Man Cave).

Figure 11. Burnt cracked stones from Zhoukoudian Locality I (Peking Man Cave).

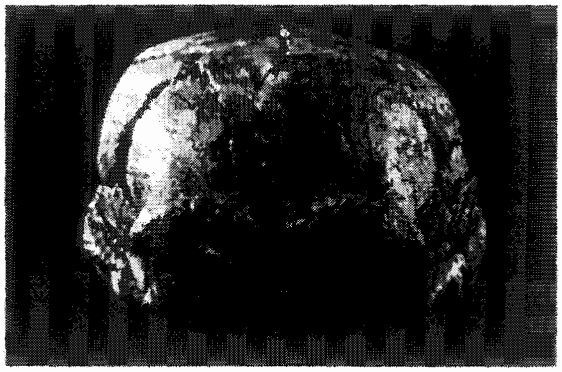


Figure 12. Frontal view of *Homo erectus* skull from Hexian County, Anhui.

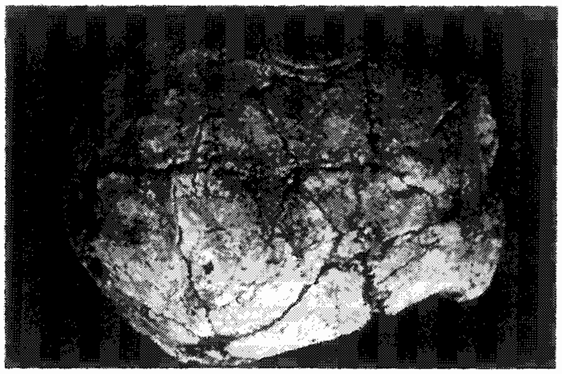


Figure 13. Top view of *Homo erectus* skull from Hexian County, Anhui.

Figure 14. Lateral view of *Homo erectus* skull from Hexian County, Anhui.

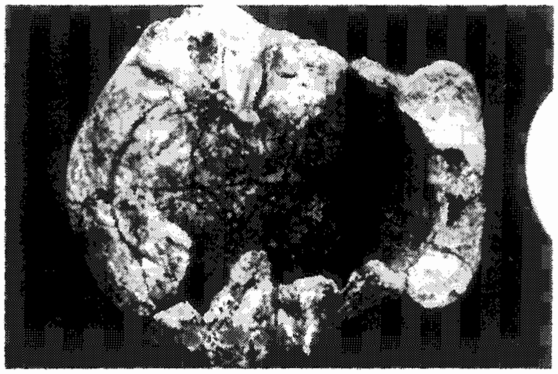


Figure 15. Basal view of *Homo erectus* skull from Hexian County, Anhui.

Hexian Homo erectus

Fossil remains of *Homo erectus* were found in Hexian County, Anhui Province in 1980. They consist of an almost complete calvaria, a fragment of the left mandibular body and several isolated teeth of one individual.

The calvaria (Figures 12, 13, 14, 15) is of a young male individual. The vault is low. The torus angularis is well developed. The temporal squama is relatively high with an arched parietal margin. The frontal is flattened and distinctly receding. The maximum cranial breadth lies at the level of the supramastoid crest. The torus occipitalis is developed and so is the sulcus supratoralis. The angulation between the upper and lower scales of the occipital is marked.

As a whole, the Hexian skull possesses many typical features of *Homo erectus*. Comparison of this specimen with other *Homo erectus* finds from China and Java indicates that it is most similar to Peking Man, suggesting a closer relationship between them.

The associated fauna include *Trogontherium cuvieri, Lutra sp., Ursus arctos, U. thibetanus kokeni, Hyaena sinensis, Homotherium sp., Stegodon orientalis, equus sp., Tapirus sinensis, Megatapirus sp., Dicerorhinus sp., Sus lydekkeri, Pseudaxis grayi, Sinomegaceros pachyoteus* etc. Based on the fauna, the geological period of this site is Middle Pleistocene.

Others

Teeth of *Homo erectus* type were also discovered in 1975 from Yunxian County and in 1976 from Yunxi County, Hubei Province and in 1978 from Nanzhao County, Henan Province. Quite recently, fragments of skull and limb bones, and isolated teeth of this type have reportedly been found in Yiyuan County, Shandong Province.

TRANSITIONAL *HOMO SAPIENS*

Dali Man

The fossil of Dali Man includes a nearly complete cranium, less the mandible (Figures 16, 17). It was found in the western part of Dali County, Shaanxi Province

According to Wu Xinzhi (1981), most features of the cranium of Dali Man are consistent with those of the specimens of early *Homo sapiens* or possibly intermediate between those of *Homo erectus* and modern man. Besides, Wu pointed out that the Dali cranium has many features in common with other human remains in China, including the presence of sagittal keeling, the maxillary sulcus and an Inca bone, the profile of the nasal bones, the orientation of the fronto-sphenoidal process of the zygomatic bone and the angled contour at the lower margin of the junction between the maxilla and the zygomatic bone.

Several hundred stone artifacts and many mammalian fossils have been unearthed from this site. The former are mainly flake scrapers and the latter include *Palaeoloxodon sp., Rhinoceros sp., Megaloceros pachyosteus, Pseudaxis cf. grayi, Bubalus sp., Castoridae, Struthio anderssoni*, etc. Its geological period is thereby dated to late Middle Pleistocene, estimated to be 0.15-0.2 mya.

Xujiayao Man

Fossils of Xujiayao Man were first found in 1974 from Xujiayao Village, Gucheng Commune, Yanggao County, Shanxi Province. Major excavations in 1976 and 1977 produced much material, consisting of fragments of parietals and occipitals, pieces of maxilla and mandible and isolated teeth. Morphologically, its features seem to be intermediate between the Peking Man and modern man. Besides, nearly 20,000 stone artifacts, lots of bone implements and a great quantity of mammalian fossils were found in this site.

The associated fauna includes *Paleoloxodon cf. naumanni, Coelodonta antiquitatis, Equus przewalskii, E. hemionus, Megaloceros ordosianus, Cervus elaphus, Spirocerus hsuchiayaocus sp. nov., Spirocerus peii, Bos primigenius*, etc. Judging from the fauna, it probably belongs to the basal part of the Late Pleistocene, estimated to be 0.1 mya.

EARLY *HOMO SAPIENS*

Maba Man

Maba Man, represented by a partial cranium, was found in Maba, Qujiang County, Guangdong Province. This was the first early *Homo sapiens* found in South China and thus enlarged the distribution of this type of early man in China. Associated mammalian fossils include the giant panda and *Stegodon* which are common in the Pleistocene cave deposits of South China.

Dingcun Man

Dingcun man includes fossils of three teeth of a child found in 1954 and a piece of parietal of a baby found in 1976 near the village of Dingcun, Xiangfen County, Shaanxi Province. Stone artifacts were found in more than ten similar sites in this area. The accompanying fauna includes *Dicerorhinus mercki*, hyena, ostrich, etc.

Changyang Man

A piece of maxilla was found in Changyang County, Hubei Province in 1956. Among the associated animal fossils are *Hyaena sinensis*, the geological age of which was dated to the Late Pleistocene.

Figure 16. Frontal view of cranium of early *Homo sapiens* from Dali County, Anhui.

Figure 17. Lateral view of cranium of early *Homo sapiens* from Dali County, Anhui.

Besides, two fossil upper incisors associated with some stone implements probably from the Middle or Late Pleistocene were found in Tongzi County, Guizhou Province in 1971.

LATE *HOMO SAPIENS*

Liujiang Man

The Liujiang Man fossils were found in a cave on Xinxing Farm, Liujiang County, Guangxi. They consist of a complete cranium, lower four thoracic vertebrae attached with rib fragments of different lengths, all five lumbar vertebrae, a sacrum, a right innominate and two femoral fragments.

The cranium (Figure 18) has many Mongoloid features, such as large and forward protruding zygomatic bones, low and wide nasal bones, a slightly concave nasal bridge, a depressed lower margin of the piriform aperture, a shallow prenasal fossa, unclear canine fossa, shovel-shaped upper incisors etc. Thus Liujiang Man was considered to be an early type of evolving Mongoloid.

The associated fauna is the *Ailuropoda-Stegodon* assemblage, commonly known from the mountain caves in South China.

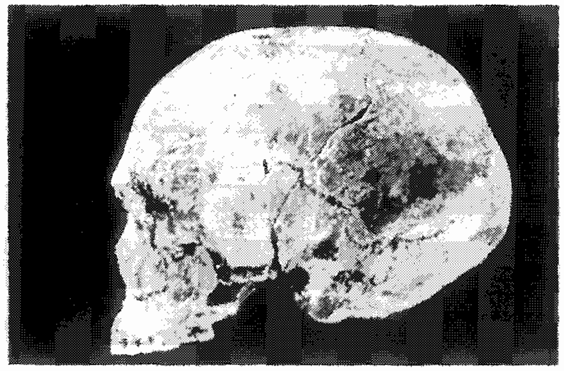


Figure 18. Lateral view of skull of late *Homo sapiens* from Liujiang, Guangxi.

Figure 19. Frontal view of skull of late *Homo sapiens* from Ziyang, Sichuan.

Ziyang Man

The Ziyang Man fossil was found in 1951 in Ziyang County, Sichuan Province. It consists of a partial cranium with its basal part mostly missing, and a maxilla (Figure 19). A bone awl was also found at this site (ibid.:148).

Upper Cave Man

The fossils of three complete skulls were discovered in 1933 in a cave above the famous Peking Man Cave at Zhoukoudian. Some bone and stone artifacts were associated. A restudy of the fossils by our colleagues showed that they are representatives of primitive Mongoloids.

"Ordos" Man

A child's upper lateral incisor was discovered among lots of mammalian fossils in 1922 at Da Gou Bay, Wushen Banner, Nei Mongol Autonomous Region. In 1956 the lower half of a left thigh bone and a part of a right parietal were found in this area.

Other late Homo sapiens fossils

Isolated skull parts, fragments of limb bones, and teeth of the Late Palaeolithic have been found in Tainan County, Taiwan Province, Jianping County, Liaoning Province, Xintai County, Shandong Provi and Yushu County, Jilin Province.

The fossils in China provide an important basis study on the origins of modern races, especially Mongoloids. It is interesting to note that the Chi hominid fossils from the earliest *Homo ere* including Yuanmou Man, right up to modern *H sapiens* including the Upper Cave specimens Zhoukoudian, all show features similar to those of Mongoloids. Fossil upper incisors from Yuan Zhoukoudian, Yunxian, Yunxi, Nanzhao, Xujia Dingcun, Tonzi, Liujiang, Upper Cave, Ordos etc all shovel-shaped. Cheek bones from Zhoukou Peking Man Site, Maba, Liujiang and the Upper are all jutting forward. The more perpendi oriental nasal bones occur in specimens Zhoukoudian, Changyang and Liujiang. The calv portion of the skull from Lantian, Zhoukoudian P Man Site, Dali, Liujiang, and Upper Cave all sh more or less marked sagittal keeling or an indicati an Inca bone. It is generally agreed that Ame Indians migrated into America from East Asia. A evidence for their ancestors have been found many sites in China. It is also interesting to note the fossil skulls found in South China show features of the Australoid race. Thus it seems tha very ancient Chinese had their own specific inhe characteristics within the Mongoloid division, but had relationships with peoples outside China.

REFERENCES

Institute of Vertebrate Palaeontology and Palaeoanthro
Chinese Academy of Sciences
1980 Atlas of Primitive Man in China. Beijing: Science Pres

Woo, Ju-kang
1962 The Mandibles and Dentition of *Gigantopi* Paleontologica Sinica (N.S.D.) 146(11):1-94.

Woo, Ju-Kang
1980 Palaeoanthropology in the New China. *In*: L.K. Kö (ed.), Current Argument on Early Man, Report f Nobel Symposium. Pp. 182-206. Published on behalf Royal Swedish Academy of Science. Oxford: Pergamon

Wu Rukang (Woo Ju-kang)
1980 Palaeoanthropology in China (1949-1979). Ver PalAsiatica 26:1-8.

Wu Rukang (Woo Ju-kang), et al.
1981 *Ramapithecus* skulls found first time in the world. Tongbao 26:1018-1021.

Wu Rukang
1982 Recent Advances of Chinese Palaeoanthropology. Oc Papers Series No. 2. Hong Kong University Press.

Wu Rukang (Woo Ju-kang) and Dong Xingren
1982 Preliminary study of *Homo erectus* remains from Anhui. Acta Anthropologica Sinica 1:2-13.

Wu Xinzhi
1981 A well-preserved cranium of an archaic type of early *sapiens* from Dali, China. Scientia Sinica 24:530-541.

Question Period III

Cooke: It's very interesting to see these Mongoloid racial characteristics appearing in the fossils. This raises some interesting ideas that one might develop. Perhaps the multiple evolution of man, maybe *Homo erectus* has given rise to *Homo sapiens* by more than one pathway. That will pose a problem for geneticists. We have a question in the back.

Question: I was wondering whether the transitional form was placed with *Homo sapiens* or *Homo erectus*?

Wu: With the early *Homo sapiens*. My former graduate student Dr. Wu Xinzhi has already published a paper in *Scientia Sinica* regarding the transitional skull.

Question: I also have a question about *Gigantopithecus* — I was wondering if you could explain to me a little more clearly, where you are placing *Gigantopithecus* in relation to the pongids and the hominids.

Wu: Well, there is the possibility that from *Sivapithecus* comes one branch to orangutan and the other branch goes to *Gigantopithecus*.

Question: So the matter is still debatable?

Wu: Yes, but we so far have only three mandibles and more than one thousand teeth, no maxillae or facial portions of the skull. According to the morphology of the teeth, it has some features of pongid and other features of hominid. And also you see in *Ramapithecus*, if we only look at *Ramapithecus*, there are many features related to the hominids, but if you consider it together with *Sivapithecus* that we have found in the same site and the same layer, many of the distinctive features are similar both in *Sivapithecus* and *Ramapithecus*. So I believe it is more related to the ancestors of orangutan than to the hominids.

Question: You also referred to the differences between *Ramapithecus* and *Sivapithecus* as possibly being sexually dimorphic characteristics. You were saying it was based on the different proportions of the teeth...are there any other features?

Wu: The proportions are similar, but their absolute sizes are quite different.

Question: So it's just basically the size differences on which you are basing this....

Wu: Not only on the size differences, but also differences in the morphological features of the facial portions. I have just mentioned the upper maxilla, the mandible and the teeth. There are differences in the cusps of the molars and other features.

Cooke: I think perhaps what is worrying people is where Dr. Wu stands finally. He suggested two alternatives that *Ramapithecus* and *Sivapithecus* might conceivably be the same species but sexually dimorphic, but on the other hand, I think he himself believes that they are in fact specifically distinct and that there are skull characteristics and facial characteristics that make it improbable also in view of the size difference that they do belong to the same species. I think we see Dr. Wu as a little worried about *Ramapithecus* not being a hominid but is not prepared to sink it with *Sivapithecus*. Am I right?

Wu: No. I've had many discussions with colleagues in paleoanthropology and the majority of paleoanthropologists believe *Ramapithecus* is still in the lineage of the hominids, but according to recent findings it seems most probable that it is not in the hominid lineage but rather related to the ancestors of the orangutan. These two types are found together. In Lufeng, many of them are in the same layer, and in many of the same sites they have both types, whether in Kenya, in Greece, in Hungary, Turkey, they have all found both types. Many of them are together. Of course one interpretation is that they are of the same type. Another is that they live in the same surroundings but in a different ecological niche, one living in the tree top, the other at the base. Within the *Ramapithecus* or *Sivapithecus* it's very difficult to differentiate the two types based on the size of the teeth. This means that there is very little or no sexual difference. In the great apes there is a great sexual difference, especially in the orangutan; the female weight may be less than half that of the male. According to Napier, the female is only 47% of the average weight of the male. So you see in the modern orangutan they have quite great sexual differences. Of course, the African apes like the gorilla also have great sexual differences, but not so great, and the chimps have much less sexual differences, so *Sivapithecus* or *Ramapithecus* are related to ancestors of orangutan. Whether we put it in the same species or the same genus according to the law of priority, it should be called *Sivapithecus* instead of *Ramapithecus*. Maybe they are of the same genus and different species. In Lufeng they may be different from Pakistan, or from Turkey. There should be further study.

Cooke: Thank you, it's clear that we should have some swords available for tomorrow morning's panel, with Professor Tobias on the attack and Professor Wu on the defence. Size after all is not all that important. One of my seventeenth century ancestors weighed 600 lbs. Do we have some more questions?

Question: I was wondering if I could ask an archaeological question of Dr. Wu? You said that there has been now a complete study done of the stone tools from Choukoutien. I believe you said about 10,000 of them. Do you know if that changes the interpretation of the stone tools from the earlier one?

Wu: Well I'm doing nothing archaeological. So far, according to the results of our archaeologists, artifacts of the lower layers are simpler, more primitive. The implements of the upper layers are somewhat more advanced. And now, I forgot to say that in our recent comprehensive project, we are still making excavations on the other half of the deposit. Formerly, we just wanted to get more material from the top to the bottom. Many of the upper layers are just stones with very few fossils. In the past three years we used the idea of horizontal archaeology as was used in Africa. So we now we are beginning to excavate from the top to the bottom, layer by layer. It takes time, and many of the upper layers are just large stones. So we are now near the cultural layer with human fossils...work is still going on. Maybe in time, maybe this year or next year we will find more skulls of Peking Man or other hominid fossils.

Cooke: Perhaps one day you'll find the hand of Peking Man with a handaxe. Are there any other questions? I see Glynn Isaac, who can't bear to hear stone implements talked about, is going to intervene.

Isaac: I want to ask about stone tools. I was just fascinated, Dr. Wu, by your account of the six metre bed of ashes. I wondered if we could persuade you to tell us a little more what is in the layers — is it solid ash; is there other material; can you see what tools are being used; do you see individual layers within it? Would you perhaps tell us a bit more about the great big hearth/ash pits?

Wu: The deposits are divided into 14 layers from top to bottom. They have identified layers that contained the hominid skull and other hominid fossils and the stone implements.

Cooke: He's asking about the details of the ash. Is there any structure within the ash, are there tools, or any other foreign things in the ash layer?

Wu: Oh yes, in the ash layer there are stone and bone implements of all sorts.

Human Brain Evolution: A Search for Units, Models and Synthesis[1]

RALPH L. HOLLOWAY
Department of Anthropology
Columbia University
NEW YORK, New York 10027

Abstract: The challenge of trying to understand human brain evolution requires a constant synthetic integration between comparative neuroanatomy and paleoneurology. Each has its strengths and weaknesses, but only paleoneurology can provide insights into an evolutionary lineage's brain evolution. The challenge in this realm is to move from "paleophrenology" to a paleoneurological domain that is empirical, quantitative, and hopefully replicable. Paleoneurology can provide at least six levels of neurobiological information. Absolute (and relative) brain size is but one level. This paper will focus on those kinds of evidence which hopefully address the issue of brain **organization** and **hierarchical** development, which might be considered as additional "phenotypic windows" worthy of study. Thus far, the evidence from paleoneurological investigations suggests that cerebral organization toward a human pattern preceded the well-authenticated increase in absolute brain size, and possibly occurred in *Australopithecus afarensis*. This organizational change is reflected in convolutional patterns, hemispheric asymmetries, and size-shape morphometric patterns as analyzed through multivariate statistical techniques. Given these aspects, analyses which examine brain size *alone* are very likely to provide misleading and possibly erroneous conclusions regarding the past dynamics of human evolution, e.g., the nature of human mosaic evolution and "punctuated equilibria" and/ or "gradualism."

Résumé: C'est sur l'intégration synthétique constante des disciplines de neuroanatomie comparative et de paléoneurologie que repose la compréhension du cerveau humain. Bien que chacune ait ses avantages et ses lacunes, seule la paléoneurologie peut pénétrer de manière empirique le développement de l'évolution cérébrale d'une lignée en pleine évolution. Le défi est de savoir passer du domaine "paléophrénologique" au domaine paléoneurologique, ce dernier étant de nature empirique, quantitative, et, nous ôsons l'espérer, reproduvisible. Plus de six niveaux d'information neurobiologique nous viennent de la paléoneurologie. Le volume cérébral absolu (et relatif) n'est que l'un de ces niveaux. Cet exposé porte en majeure partie sur les données se rapportant à la question de l'*organisation* du cerveau et de son développement *hiërarchique*, lesquels peuvent être considérés comme "fenêtres phénotypiques" et valent la peine d'être étudiées. D'après l'information paléoneurologique actuelle il semble que l'organisation cérébrale menant vers des aspects humains ait pu se produire chez l'*Australopithecus afarensis*. Ce changement au niveau de l'organisation cérébrale est traduit par l'aspect des circonvolutions, certaines asymétries hémisphériques, ainsi que par les aspects morphométriques de forme et de volume tels qu'analysées par les technqiues de statistiques à variables multiples. Comme on peut le voir, les études qui se concentrent *uniquement* sur le volume cérébral peuvent facilement projeter des conclusions trompeuses ou même erronées concernant les forces motrices de l'évolution humaine comme, par exemple, sur la nature de l'évolution humaine composée et "l'équilibre ponctué" et/ou le "gradualisme".

Keywords: **Human brain, evolution, neuroanatomy, paleoneurology.**

INTRODUCTION

Brain endocasts provide notoriously little information about brain organization, and yet their existences are often seized upon to discuss the evolution of the human brain. In essence, the most secure datum provided by an endocast (which is only a mold of the interior table of cranial bone) is its volume. And except for paleoneurological specialists, who could all fit in one telephone booth, **size** or **volume** of the brain would appear to be the sole phenotypic manifestation of any value to understanding human evolution. A roughly 3-to-4-fold increase in brain size during the past 4 million years, from some *Australopithecus* species (*afarensis*) to *Homo sapiens sapiens* cannot be taken lightly. That **was** a dramatic increase in the size of a very expensive metabolic organ, or better, set of organs. If this tendency to consider brain size alone were applied to other morphological components of human and other primate evolution, e.g., the limbs, dentition, cranium, etc., imagine how impoverished our understanding of primate evolution would be. Is size the singular phenotypic manifestation of complex ontogenetic and phylogenetic processes ascertainable from comparative neuroanatomy and paleoneurology? Are evolutionary selection models predicated purely on "allometry" or "information processing" sufficient explanations of human brain and behavioural evolution? Are these models truly testable, i.e., refutable, when we have scarcely a single accurate body weight to associate with any particular hominid cranial capacity?

After years of collecting information from comparative neuroanatomy, do we even know **what** varies phenotyptically in different animal species regarding CNS structures, or how that variability relates to behaviour at the species-specific level, or how natural selection operates at the genotypic level affecting neural phenotypic variability?

Taking our own species as an example, I would challenge anyone to provide authentic, replicable, empirical evidence that can relate normal brain size variation to behavioural variation.[2] Yet the literature is replete with examples of the continual utilization of these two gross levels of distal phenotypic manifestations as if they were, in and of themselves, the only genotypic variations under pressure of natural selection, or other evolutionary mechanisms, such as drift, mutation, etc.

My purpose in participating in this symposium is not to provide a neat theory, but rather to express a number of reservations I have regarding the ways in which the problem of human brain evolution are approached. My purpose is to try to delineate some of the problems, as well as provide what I hope are some fresher insights from the paleoneurological evidence for hominid brain evolution during the past 3 to 4 million years.

EXPANDING THE PHENOTYPIC WINDOWS

I begin this paper with a fairly long quotation from a recent article entitled "Gene Expression in Brain" (Farquhar, et al. 1979) because it offers so much protein for thought:

> "Gene expression in mammalian brain is higher than in other complex tissue. DNA-RNA hybridizations studies with adult mouse, rabbit and human brain RNA have shown that 25% to 40% of single copy DNA...is expressed as RNA in brain compared to 10% to 12% in liver, kidney or spleen...Much of the transcribed RNA is degraded in the nucleus...;however, about 20% of the various sequences are transported to the cytoplasm for use in protein synthesis...the high level of transcription in the brain represents a capacity for expression of thousands of different DNA sequences...Studies of gene expression at different stages of normal and abnormal development suggest that brain development is associated with large changes in gene expression. Comparisons of RNA diversity in fetal and adult mice...,rabbits..., and humans...show that twice as many sequences are expressed in the adult as in the fetal brain...Studies of gene expression in rat brain have demonstrated differences based on environmental rearing conditions. For example, brain RNA from rats raised in impoverished environments show less sequence diversity from littermates raised under enriched conditions...Approximately 95% of (single copy) DNA sequences are homologous between chimpanzee and human and 85% are homologous between macaque and human...whereas less than 5% are homologous between rodent and human..."

First of all, the brain shows a 2 to 4-fold increase of DNA (single copy) expression over most other organs. This convincingly suggests more structural genes for natural selection to act upon. There is a 2-fold difference in expression of RNA between fetal and adult brains, and part of the diversity of RNA is attributable to environmental influences. In other words, a considerable amount of genetic switching "on and off," and integration takes place. Given a 95% homologous rate between ourselves and chimpanzees, one wonders what the 5% controls, particularly in view of the known prolonged growth of the human brain after birth in comparison to the chimpanzee. The majority of papers in the literature concerned with human and/or primate brain evolution give the implicit suggestion that the above 5% only regulates the size of the brain. There is not a single empirical demonstration that this is the case.[3]

Numbers have an almost magical quality about them, particularly for those concerned with phenotypic windows that lead to theories regarding brain evolution. Thus brain size, relative brain size, and derived statistics such as E.Q.'s (encephalization quotients) and Nc's ("extra neurons") (Jerison 1973) have been the most widely and persistently used phenotypic windows to express our wider ignorance of the total phenotypic expressions inherent in brain structure and function. To put it more bluntly, we must get beyond these phenotypic expressions of **size only**, if we are ever to have a coherent theory about human brain evolution. One could say the same for aardvark brain evolution, or brain-behavioural relationships in different breeds of dogs. I am not knocking or ignoring brain size; I am indicating that we must look for more than size, and give more thought to what natural selection actually works upon: the size of the brain, or all the complex unfolding of gene expression during differentiation, development, and growth of the brain in different species, the **most distal expression of which is brain size.**

In 1979, I tried to express my thoughts about these problems as follows:

> "By cathecting on size alone, all evolutionary paradigms become reduced to natural or genetic selection operating on incremental size increases and behavioural efficiency, which always has the underlying implicit structural argument that 'intelligence' equals 'brain size.' Thus, for example, all hominid evolution becomes 'scaling,' 'allometry,' or quantitative increases, whereas these are only distal manifestations of something more complex and important. In other words, all of individual variation, the very stuff that evolution works on, is reduced to a single dimension of either small or large. In fact, it is likely that the selection events in any animal's life depend more on the timing of maturational events, epigenesis within the central nervous system (CNS), and everyday events—that is, the 'nitty-gritty' life-death 'selection walks'—are matters of hierarchical organization, differentiation, and development, of which the outcomes through time can only be measured (thus far) as size increments. We should and can demand richer explanations." (Holloway 1979: 85).

BRAIN SIZE AND TIME

There have been a number of attempts to plot the known increase in hominid brain size vs. time. The attempts are worthy, motivated by the desire to see graphically tempo and mode in the evolutionary history of this complex organ, and thus hopefully glean some insight into the selection dynamics operating in the past. Figure 1, adapted from Holloway (1972), shows one such attempt to provide a conceptual basis for trying to depict such changes, and offers a number of possibilities. I believe it is only fair to say that such efforts are very premature, given the paucity of endocranial brain volumes and truly reliable absolute chronometric dates. The fossil hominid record does not presently suggest any single line of evolutionary development that is without controversy, making it thus impossible to put what few early endocranial volumes that exist into some neat and orderly phyletic sequence of pleasing anagenic simplicity.

The earliest hominids yet discovered date to about 4 mya (million years ago), and are from the Hadar region in Ethiopia (Johanson, et al. 1982), and Laetoli, Tanzania.[4] The range of size difference in postcranial bones and dentitions is immense, but there is only **one** cranial portion that permits a reasonable **guess** at this creature's brain size. It is about 500 ml, based on a preliminary reconstruction I have made at Columbia University. That is, unfortunately, not enough to go on, as the body size estimates are quite variable. I will discuss certain morphological aspects of this endocranial brain cast somewhat later, but for the purpose of this section, it might tentatively be suggested that if the

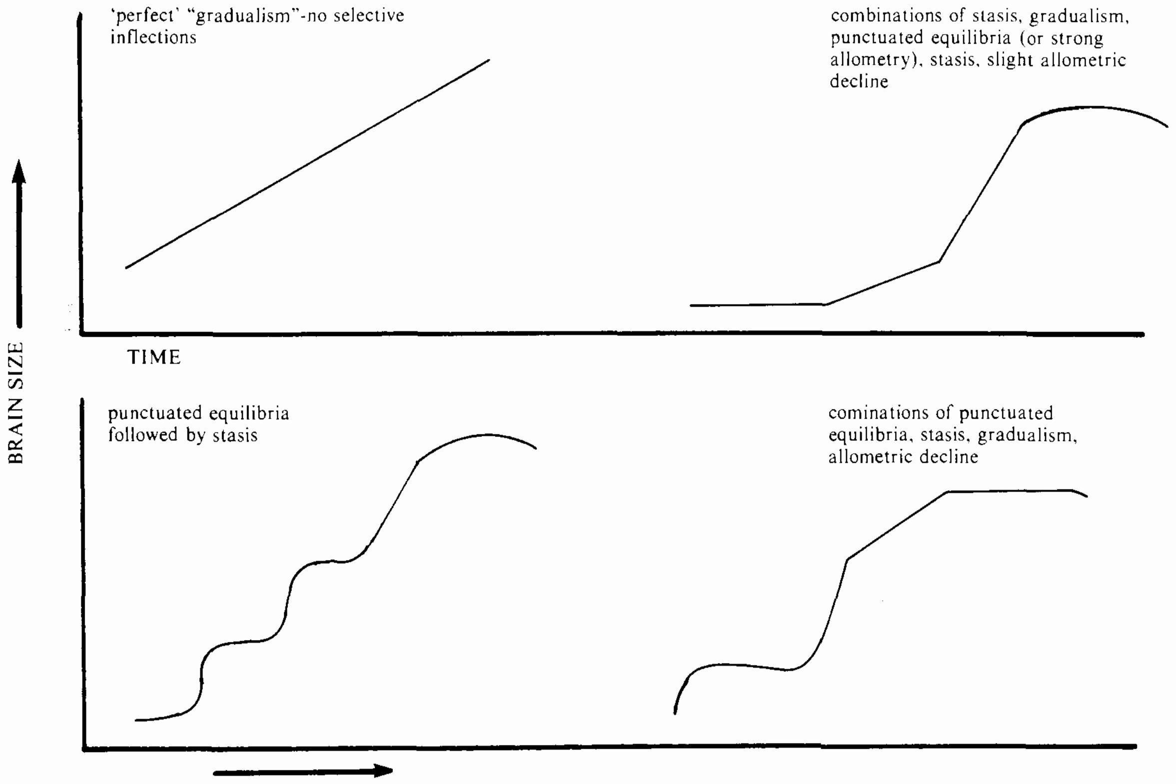


Figure 1. These hypothetical brain size versus time curves depict four possibilities during hominid evolution (adapted from Holloway 1972). Curve A would obtain if only allometrical change took place within a single hominid lineage, and at a constant rate, reflecting increasing body weight. Curve B is a composite, reflecting initial stasis, a gradual increase through allometry, and then "punctuated equilibria" where brain size increases dramatically, either through "strong" allometry, brain size increase without significant body size increase, or both. The slight allometric decline is suggested for the Neanderthal to modern *Homo sapiens* decrease. The first segment might represent *A. afarensis* with a gradual allometric (or isometric brain increase) to *A. africanus*. The strongly inclined segment could represent a *Homo habilis* to advanced *Homo erectus* evolutionary period. **However**, without secure knowledge regarding body size changes which would affect relative brain size, or reorganizational changes (e.g., increased parietal association cortex, hemispheric asymmetry, etc.), or changes in hierarchical development, these curves could be entirely misleading, as only the most distal phenotypic manifestation of neurogenetic processes is being plotted, i.e., brain size. Furthermore, the possibilities of different co-existing lineages are not drawn. Curves C and D are simply additional possibilities. The point is, we do not have the requisite knowledge to draw such curves, let alone understand their meaning in terms of evolutionary dynamics, and the paleoneurological evidence is suggesting that other changes besides brain size took place.

body-size estimate of about 75 lbs. is correct, the relative brain size of this Hadar adult *Australopithecus afarensis* is advanced beyond the chimpanzee level.

But it should be a matter of some reflection as to what brain size vs. time tells us; given a plethora of brain endocasts, all accurate with regard to volumes, and highly accurate body weights, and times, what would we have? We would have a basis for speculating about the reasons behind the **inflections** (or lack of them) in our curves of brain weight vs. time. We might speculate that at time X_1, brain growth was purely allometric, i.e., related to body size; while at time X_2 it was isometric; or at time X_3, increased without concomitant increase in body size. We could say the speed of change was fast here, slow there, constant here, etc., etc. and invariably, we would be trying to relate the **adult** volumes to behavioural efficiency and adaptation, and our model would still be one of natural selection operating on brain size only. The implicit or explicit assumption behind all of this would be: "bigger **adult** brains, better **adult** behaviour." Behaviour might be fragmented into modes of cognitive functioning, such as "memory," "foresight," "planning," "delay between stimulus and response," etc., etc. Any differences between brains in either cerebral organization or hierarchical development would not be included in the plot, and thus significant selection points possibly missed.

Let me put this another way. Imagine a line of finite length, L, representing the time of conception at the beginning, the time of death at the end, and in between we could mark off particular landmark events representing the ontogeny of a single individual. At some point, we would make a mark for reproduction, since that is the most critical time which the organism must exceed if its genes are to be replicated in the future. For a male, it may or may not matter whether the time extends further. For the female, it definitely does. Now that whole line, however long it is drawn, is subject to natural selection, and what bothers me most frankly is that most of our thinking is directed toward that line segment which extends beyond reproductive capability. To my mind, in species such as primates, and ourselves in particular, there is a relatively **long time** during which the organism must survive if it is to pass on its genes, and most of that time the organism is dependent on other social actors in its group. There is no point in denying that natural selection can operate on behaviour in the adult. My point is that natural selection also operates on a most complex interactive and interdependent set of developmental processes during the maturation of the brain **and its social and material nourishment**.

Our pictures of brain size vs. time cannot contribute to those developmental complexities in any meaningful way, except by realizing that the most distal expression of those processes is adult brain size, and that **sum**, I would argue, is really far less interesting than the parts that went into making the whole. I hope my intention is clear; by all means, we must and will continue to study brain size, but let us not lose our perspective as to what **that** phenotypic expression implies. For one thing, it implies a large number of supportive or complementary social behavioural adaptations and biological sequelae to accommodate the final product. The blood supply, pelvic diameters and flexibility during parturition, social care and nourishment, "learning," behavioural patterns emergent with extended growth and developmental periods, both in terms of extracting adequate energy resources from the environment (gathering and hunting), and a socially responsive network of caretakers, are only some of the most obvious supportive adaptations one can imagine.

ALLOMETRIC CONSTRAINTS

I believe that much more serious thought must be given to our allometric models.[5] For example, consider Jerison's (1973) magnificent chart in which 198 vertebrate species are plotted, brain weight against body weight. A polygon emerges, and by a critical geometrical choice, a slope of .66 is drawn through the array. Some of the species plotted are closely related to each other, others are not. The conclusion reached is that the brain and body are allometrically related in all species, and different brain sizes emerge from selection on body size. The question arises, or at least should arise, "how can one test the proposition that the relationships between brain and body weights is allometric for any group of phylogenetically related species?" Does every instance of a point laying on a trend line, or close to it, necessarily mean that only two variables are causally interacting? Could not some points lie on the line because indeed the former is the case, while others approximate the line for different reasons? How can one test the question? If we look at the scatter of points, particularly when log-transformed, it has a pleasing "groupiness" to it. But empirically, one should calculate the difference between the observed and predicted values for each species, and indicate closeness of fit. As far as I am aware only Passingham[6] and myself have tried to do this task for the primates. And when it is done, neural structure by neural structure, against either body weight or brain weight, there are some interesting departures between expected and observed values.

This does not deny value to the allometric concept, its definition, and its application to diverse data to take into account size increases. But I detect a tendency to reify such expressions to an almost genetically real level. Facetiously, I once said (1979: 64): "While I have never seen reference to a '.66 gene,' I believe most people think in those terms." I regard allometry as a preliminary descriptive depiction of the **correlative** nature between two complicated phenotypic characters, e.g., brain weight and body weights, or volume of primary visual cortex and brain weight, etc., etc. I do not regard it as a cause-effect analysis. For me, any allometric trend line is a **constraint, about which real organisms vary.** I regard the variations as no less important than the overall constraint, for it is the species-specific departures from trends which interest me, and for the time being, that interest happens to be focused on the human species. Perhaps tomorrow, it will be the aardvark, hyaena, or whatever species.

Surely by now, after decades of fascinating behavioural observations of different animal species both in their natural and laboratory settings, we have come to realize that each species is somehow unique in its total behavioural repertoire, and yet there are very broad regularities, samenesses, universals if you prefer, which also exist, for example, in the mammals. These are not trivia, they are the substance of natural selection working over millions of years to produce variations upon which future selection will continue to work. They are not thoroughly explainable through allometry. All that can **possibly** be explained through allometry is adult brain size, a phenotypic characteristic which can be obtained through a diversity of developmental processes. If we were to plot all of the mammal species on a large diagram and throw in the values for cocker spaniels, great danes, basenji hounds, terriers, collies, and poodles, would anyone seriously expect them to deviate significantly from a mouse-whale plot of brain size and body weight? If you added alley and Siamese cats, would you expect any radical departures? If you added brown, black and the S-1 strain of rats, would it make a difference? Would you seriously propose that allometry "explains" their various behavioural and temperamental profiles?

Why then, should *Homo erectus* simply be an allometrically scaled version of *Australopithecus*, when the former made stone tools to standardized patterns and hunted large game animals, while there is no evidence that the latter did the same? Why should *Australopithecus robustus* be merely an allometrically larger version of *Australopithecus africanus* simply because brain size and body weight are larger in the former? Their teeth are not simply allometrically different, nor are their pelves, nor are the taphonomic relationships similar in the different beds in which they are found. Nor does the shape of the dorsal portion of their endocranial casts lend itself to such an interpretation (Holloway 1981), or the venous drainage through a marginal or accessory sinus in the robust and *afarensis* groups (see below).

Some extremely interesting and controversial work has been done by D. Freedman at the University of Chicago on ethnic differences in newborn behaviour in humans (Freedman and DeBoer, 1979). Are these differences, mostly in temperamental attributes and motor development to be related to brain size, or slight variations in the timing sequences of differentiation, development, and maturation of different parts of the newborn central nervous system? How much of the 25% to 40% of single copy DNA is involved in such variation? How much of the 20% of transcribed RNA sequences are involved? How much of the 5% difference between ourselves and chimpanzees single-copy DNA is involved? Intriguing questions perhaps, but no answers are available. The point is, there does exist some evidence for phenotypic variation of brain-behavioural interrelationships, and this work, if replicated and enlarged, could throw some much needed light on neurological variables other than size[7].

If, as de Lacoste-Utamsing and Holloway (1982) suggest, there is a statistically significant, measurable sexual dimorphism in the human corpus callosum, how much is allometric and how much controlled by genetic and epigenetic events during maturation of the brain? And when, out of a sample of almost 150 primate endocasts, we find striking differences in asymmetry patterns between pongids and humans in their cerebral hemispheres are we to regard these variations as only examples of allometry? (Holloway and de LaCoste-Larymondie, 1982)[8].

Allometry is a proper **first** approximation for testing the mathematical relationships between two variables, and thence for framing testable hypotheses about the causal (not merely correlative) association between them. This is the value of Jerison's work, and that is admirable. My point, however, is that any full evolutionary description of brain evolution will have to include more than allometry, and we must find ways of exposing **other** phenotypic windows on the brain and its development to achieve any holistic, synthetic theory between behaviour, brains, and evolution.

THE PALEONEUROLOGICAL EVIDENCE FOR HOMINID BRAIN EVOLUTION

Endocasts are very imperfect sources for detailed studies of brain structural changes through time. After all, one cannot hope to study more than surface details on the cerebral cortex, **if** these impress themselves on the internal table of bone of the surrounding cranium.[9] Cranial nerves, meningeal patterns, asymmetries, morphological shape **and size** are additional phenotypic expressions of interest to the paleoneurologist. I will not detail here the appalling lack of cerebral convolutional detail that is found on most hominoid (pongid and hominid) endocasts, as that has been discussed elsewhere (e.g., Holloway 1978b, 1975).

It is an ironic fact, at least with regard to my earlier discussions about brain size, that **that** phenotypic character is simply the most available or determinable character of them all. The point is **not** to ignore size, but to attempt to use it judiciously.

In outline, there are at least six "kinds" of information available from endocasts:

1. Absolute size
2. Relative size, when postcranial remains exist;
3. Convolutional patterns; sometimes present, but rarely so;
4. Lobar division, depending on the presence of convolutional patterns;
5. Morphometric properties, such as indices, radial and linear distance, asymmetries, etc.;
6. Meningeal (and other blood supply) patterns.

One could add a seventh kind of information if one wanted to include cranial foramina, and cranial nerves. All of these "kinds" of information depend on the completeness of the endocast, the degree of cranial deformation during and after death, and the intactness of the internal table of bone.

Presently, there are only some 40 to 50 endocasts of fossil hominids available for study, and most of these are incomplete. The number of these endocasts bearing any sulcal-gyral relief are much, much less. The "perfect" endocast, one that is complete, with good convolutional relief, has yet to be discovered.

TABLE 1

Endocranial Volumes of Reconstructed Hominid Specimens

Specimen	Taxon	Region	Endocranial Volume in Milliliters	Method[a]	Evaluation[b]
Taung	*A. africanus*	South Africa	440[c]	A	1
STS 60	*A. africanus*	South Africa	428	A	1
STS 71	*A. africanus*	South Africa	428	C	2-3
STS 19/58	*A. africanus*	South Africa	436	B	2
STS 5	*A. africanus*	South Africa	485	A	1
MLD 37/38	*A. africanus*	South Africa	435	D	1
MLD 1	?	South Africa	500+20	B	3
SK 1585	*A. robustus*	South Africa	530	A	1
OH 5	*A. robustus*	East Africa	530	A	1
OH 7	*H. habilis*	East Africa	687	B	2
OH 13	*H. habilis*	East Africa	650	C	2
OH 24	*H. habilis*	East Africa	590[d]	A	2-3
OH 9	*H. erectus*	East Africa	1067	A	1
OH 12	*H. erectus* (?)	East Africa	727	C	2-3
ER 406	*A. robustus*	East Africa	510+10	D	2
ER 407	*A. robustus*	East Africa	510[e]	B	2-3
ER 732	*A. robustus*	East Africa	500	A	1
ER 1470	*H. sp?*	East Africa	752	A	1
ER 1805	*A. sp.?*	East Africa	582	A	1
ER 1813	*A. sp.?*	East Africa	510	A	1
ER 3733	*H. erectus*	East Africa	848[f]	A	1
ER 3883	*H. erectus*	East Africa	804[f]	A	1
OMO 338	*A. sp.?*	East Africa	427	C	1-2
HE 1	*H. erectus*	Indonesia	953[f]	A	1
HE 2	*H. erectus*	Indonesia	815[f]	A	1
HE 4	*H. erectus*	Indonesia	900[f]	C	2-3
HE 6(1963)	*H. erectus*	Indonesia	855[f]	A	2
HE 7(1965)	*H. erectus*	Indonesia	1059[f]	C	1-2
HE 8(1969)	*H. erectus*	Indonesia	1004[f]	A	1
Salè	*H. erectus*	Morocco	880	A	1
Solo I	*H. erectus soloensis*	Indonesia	1172	A	1
Solo V	*H. erectus soloensis*	Indonesia	1250	A	1
Solo VI	*H. erectus soloensis*	Indonesia	1013	A	1
Solo X	*H. erectus soloensis*	Indonesia	1231	A	1
Solo XI	*H. erectus soloensis*	Indonesia	1090	A	1
Spy I	*H. sapiens neanderthalensis*	Europe	1553	A	1
Spy II	*H. sapiens neanderthalensis*	Europe	1305	A	1
Djebel Ihroud I	*H. sapiens neanderthalensis*	Morocco	1305	A	1

[a] A, direct water displacement of either a full or hemiendocast with minimal distortion and plasticine reconstruction; B, partial endocast determination, as described by Tobias (1971); C, extensive plasticine reconstruction, amounting to half the total endocast; D, determination based on the formula $V=f\frac{1}{2}\,(LWB+LWH)$, Holloway (1976), where L=maximum length, W=width, B=length, bregma tex to deepest part of temporal limit of cerebellum, H=vertex to deepest part of temporal lobe and f appears to be a taxon specific coefficient.

[b] An evaluation of 1 indicates the highest reliability, 3, the lowest.

[c] Postulated for adult-the value of the actual specimen is 404 ml.

[d] Possible overestimate

[e] Provisional estimate

[f] These values, while published, have not been described and should be regarded as provisional.

Table 1. provides a list of endocasts this author has studied, giving the location (discovery), taxonomic assignment, volume, and comments about the reliability of such figures. The earliest hominids of Hadar, Ethiopia, and Laetoli, Tanzania, are still in the process of study. Laetoli, rich in footprints and mandibular and dental fragments, is without an "endocastable" cranial fragment. The Hadar region has provided three cranial fragments, none complete, of which one yields a reliable estimate. (See above.)

Taken all together, this collection indicates that absolute brain size roughly tripled during the past 3 to 4 mya, from about 450 ml (as an average Australopithecine value) to roughly 1400-1450, ml among our own modern species, *Homo sapiens sapiens*. Neanderthals, existing approximately 40 to 50 thousand years ago, did (on the average) appear to have slightly larger brain volumes, with the male average being around 1540+ ml. They also had a massive musculo-skeletal framework, suggesting a high degree of lean body mass, and from known relationships between brain size, stature and weight in modern *Homo sapiens* (Holloway 1979b), it would appear that the Neanderthal average excess above our own in brain size was probably related to its greater lean body mass, i.e., a true allometric relationship. Certainly, no significant convolutional details, or shape patterns, differ between ourselves and Neanderthals.[10]

Relative brain sizes, i.e., the ratio of brain weight (g) to bodyweight (g) can only be estimated in most cases. Our own relative brain size is large among mammals, but not the **largest**, being exceeded by a number of animals, including some primates. The Australopithecines, whether *afarensis, africanus*, or *robustus* species, are problematical, given the incompleteness of postcranial remains in **direct** association with the cranial fragments that permit brain volume to be determined. Estimates of body size do not appear to be an area where physical anthropologists share much agreement.[11] But I do believe that the available evidence is very suggestive that relative brain size is somewhat greater than the chimpanzee, our closest living primate relative. If my calculations are correct, even the *afarensis* taxon had a higher relative brain size than pongids, although its absolute brain size is overlapped by modern pongid values.

These observations have considerable relevance to other neural measures, such as E.Q.'s (encephalization quotients), which take into account both absolute and relative brain weight. The E.Q.'s scores are of course dependent upon the data bases chosen to calculate the E. Q. 's, e.g.,

$$\text{E.Q.} = \frac{\text{brain-weight}}{0.12 \text{ body wt.}} \ .66$$

The above equation was offered by Jerison (1973). Holloway and Post (1982) have reviewed the uses of different data bases recently, and we find one constant fact, regardless of which taxa are used in the data base, or which E.Q. equation is derived. The earliest hominids are always intermediate between present-day pongids and ourselves. We believe this to mean, minimally, that natural selections did operate on brains quite early in hominid evolution. I have said "brains" rather than "brain size" quite purposefully, because it is not possible to rule out organizational changes of the early hominids beyond a pongid level. With equal force, one cannot prove that anything else but size did change. In any event, the evolution of absolute brainsize is **not** a terminal dynamic in hominid evolution, although its importance was probably greater toward the middle and end of our evolutionary development.

Convolutional detail is difficult to extract from endocasts, and controversy is still in progress regarding Dart's (1924) original Taung discovery *Australopithecus africanus*. The major controversy centres about objectively demonstrating the position of the infamous lunate sulcus, or "affenspalte." If anterior, as Falk (1981) claims, the lunate is in a pongid position.[12] If posterior as I claim (Holloway 1982) and as did Dart, Schepers and Le Gros Clark, it is in a hominid position. The lunate sulcus is roughly the anterior boundary of the primary visual striate cortex.[13] If the lateral extent of that cortex appears reduced, it suggests an increase of the adjacent parieto-temporal "association" cortex. If that could be unequivocably demonstrated in *Australopithecus*, it would indicate that natural selection **did** operate on the **organization** of cerebral cortex, as well as its size, *early in hominid evolution.*

Preliminary studies on the Hadar *A. afarensis* endocast materials are provocative in at least two aspects. First, the small adult AL 168-28 portion is the best preserved specimen for endocranial detail in the posterior parietal and occipital regions. There is very clear evidence for a furrow or groove running obliquely from just anterior to the lambdoidal sutural remnant, diverging slightly from the midsagittal plane, for approximately 2 cm. It could be one of two critical sulcal landmarks: the lateral calcarine, or the interparietal. Comparisons, both morphological and metrical, with five *Pan troglodytes* brain casts (not endocasts) suggest very strongly that this feature is the interparietal sulcus. If correctly identified, the posterior portion of this groove is located in a posterior, decidedly non-*Pan* orientation. That is, since the posterior end of the interparietal **always** abuts the lunate sulcus in *Pan*, this latter feature should be more posteriorly oriented, i.e., in a human-like position, rather than anterior as in all *Pan* brains ever examined.

This is a preliminary judgement. A fuller description is currently in progress, but if correct, the significance is very great. It would mean that by roughly 3 mya, the cerebral morphology of these earliest bipedal hominids was already moving toward a truly hominid disposition, **despite the small size of the brain** (i.e. within modern *Pan* limits).

The second interesting aspect of the Hadar endocranial remains is that two specimens, the adult AL 333-45, and the infant, AL 333-105, show unambiguous evidence for marginal (or accessory) sinus drainage, which skirts the lateral internal margins of the foramen magnum. This feature, amongst hominid fossils, occurs **only** in robust forms of *Australopithecus* from S. Africa (Swartkrans, SK 849, SK 1585), Tanzania (O.H.5. — see Tobias 1967 for a detailed study), and Kenya (KNM-E.R. 407, 732). The KNM-ER 406 specimen is filled with matrix so this feature cannot presently be seen. The heart-shaped foramen magnum is so similar to that for O.H.5, that I would be quite amazed if KNM-ER 406 did not show a marginal sinus pattern also.

I do not wish to enter into taxonomic disputes at this stage, since this work is of a preliminary nature. But I do find it very difficult to accept the hypothesis put forward by Johanson, et al. (1982) that *A. afarensis* first evolved into *A. africanus*, and from the latter arose *A. robustus*. There is no evidence for a marginal sinus in any *A. africanus* specimen that I have seen. The feature, which presumably has some genetic developmental basis, would have had to appear independenty in *A. robustus* after the loss of the feature in *A. africanus*. Consequently, I favour, for the time being, an hypothesis in which both *A. africanus* and *A. robustus* are splitting off from *A. afarensis* somewhat earlier. But where is there early (i.e., ca.3 mya) evidence for a *robustus*-like lineage, unless perhaps, *A. afarensis* is ancestral to it, *or* the Hadar dates are too early?

But this is not the whole picture. Morphometric studies published elsewhere (Holloway, 1981) are showing considerable promise in more objectively ascertaining which regions on the dorsal brain endocast surface appear to show the greatest shape changes between taxa, once size is taken into account. In this regard, dorsofrontal and parieto-temporal-occipital regions appear to show the most differences in shape between extant pongids and early hominids (see Figure 2.). That is, once allometric corrections are made for radial distances from the surface to a homologous centre point, these regions still show the highest F-ratios of between-group variance to within-group variance, and can help discriminate taxa of endocasts with high degrees of correct classifications. This is provocative, but many caveats are in order, and the reader is urged to examine the original report

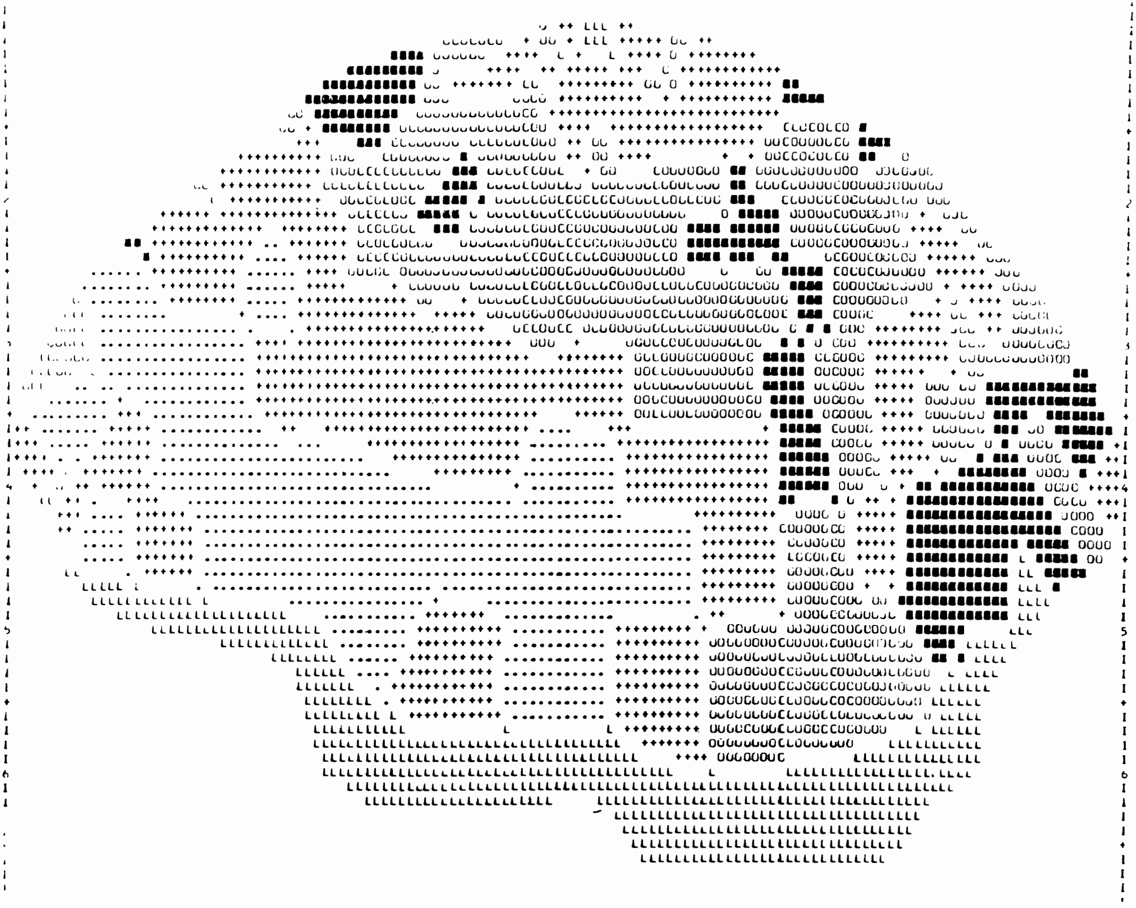


Figure 2. One of several endocast contour maps derived from stereoplotting studies (Holloway 1981a). This particular map shows the distribution of 171 univariate F-ratios, after each location was allometrically corrected (i.e., size removed). The darkest regions have the highest F-ratios (e.g., 8.5 to 12.7), significant at the .00001 level, and are located in the parietal, occipitoparietal, and middle dorsofrontal regions. This map combines information for 92 endocasts of living and fossil hominid species. The extant species were *Gorilla*, *Pan* (*troglodytes* and *paniscus*) and modern *Homo sapiens*. In essence, this map shows that the ratios of between-group to within-in group variances are very high at particular locations. Each group or set of groups compared generates a different contour map, and the reader is advised to consult the original publication for the explanation of techniques and caveats.

(Holloway 1981a). Other regions **do** show some allometric increase, and thus the studies strongly suggest that **both** size and shape were critical components during hominid brain evolution.

Moreover, studies of petalial asymmetries on a large sample of pongid and hominid endocasts (Holloway and de La Coste-Larymondie 1982) are showing significant differences in asymmetry patterns. We find that pongids, (in particular *Gorilla*), do show occipital petalial asymmetries, but seldom show the typical left-occipital, right-frontal torsion petalial asymmetry pattern so common in modern *Homo sapiens*, as Lemay[14] and her colleagues have shown. The fossil hominids, perhaps from *Australopithecus* on, but certainly *Homo*, show the human pattern with such frequency as to be indistinguishable from modern *Homo sapiens*, at least as far as Chi-square statistics are concerned.

While this finding was not totally unexpected, its strength was **not** anticipated. Considerable caution is necessary in interpreting these findings. On the one hand (to be somewhat facetious), these patterns show a high statistical correlation with right-handedness (albeit the relationships between petalias and handedness are not obligatory) and cerebral dominance. This suggests cognitive patterns of symbol-manipulating on one side, and spatiovisual and manipulovisual integration on the other, and all that **that** implies from the split-brain research of Gazzaniga, Sperry, etc.[15] These kinds of findings are ripe for synthesis with the archaeological evidence for behavioural patterns that existed among our hominid ancestors, such as tool-making, social communication (verbal and nonverbal), and skills in spatial orientation relating to throwing objects at moving targets with accuracy and force, locating game and other natural resources, and finding one's way back to camp, homebase, water source, or sleeping trees, wherever one's group was. The other hand, of course, is how to empirically demonstrate these relationships, and apply them to prehistoric populations in an evolutionary paradigm. The sample sizes for the various hominid taxa are not large enough to be certain, and in many cases, the endocasts are not complete enough to allow totally unambiguous determinations of laterality and petalial configurations. Consequently, these ideas are only tentatively offered as a basis for speculations (Holloway 1976a, b, 1981b).

Nevertheless, such observations do bring into focus the possibility of finding something other than brain size to talk about. One might ask, how far back in hominid evolution do these petalial patterns appear? With the *A. afarensis* material currently available it is impossible to tell, although it is provocative.[16] The *A. afarensis* material from S. and E. Africa is too fragmentary and small in sample size to be definitive, but the suggestion of a left-occipital petalia is very strong. By *Homo erectus* times, meaning roughly 2 mya, the evidence for a completely *Homo sapiens* pattern is very strong. This is also the time from which we have the beginnings of secure evidence for stone tool making and hunting behaviour. I personally believe that natural selection worked on the cerebral asymmetries in *Australopithecus africanus*, but that is a bias; the present evidence is simply too scant.

My theory is that natural selection has been working on brain evolution from the very beginning of hominid evolution and that the major force of selection pressures has been in the realm of social behaviour (Holloway 1969, 1970, 1975, 1981b). I also believe that selection pressures on brain organization and **size** continued throughout most of hominid evolution, at least up to Neanderthal times. I see no evidence of any significant evolutionary change from Neanderthal, or archaic *Homo sapiens* of perhaps 120,000 years ago, to modern *Homo* in brain organization or size. Of course, human evolution was **mosaic**, but I find **mosaics** within the overall mosaic which involved the brain. Thus the brain was not a terminal organ to evolve in the overall mosaic of human evolution, unless of course, one is talking only about absolute brain size, and wishes to ignore **relative** brain size, cerebral cortical organization, and cerebral asymmetry.

TOWARD A THEORY OF HUMAN BRAIN EVOLUTION

In the preceding pages, I have tried to indicate the nature of the paleoneurological evidence, and my concern with the "phenotypic window" of size as a sufficient variable. My point has been that size alone is an insufficient (although necessary) variable if we wish to understand either human behaviour or the evolutionary history of its major effector organ, the brain. Thus in addition to size, I believe we must also examine the organization of the brain and its hierarchical, or neuro-ontogenetic development.

Figure 3 is a model I tried to put forth in 1979 in order to conceptualize the problem. Like all models, it is too simplistic in some ways, and too complex in others. Let us imagine a brain, or machine, with Nx number of components, and Fy number of communicating fibres between the components (see Figure 4). This brain develops in an environment having both material and social vectors or fields. We can imagine enlarging the machine isotypically, so that our number of components, Nx, stays the same, but that the parts of the components, the nerve cells, increase in number, and that Fy increases proportionally. This is basically an allometric model (A). Or we can imagine a brain of Nx components, Fy fibres, changing non-isometrically so that one (or several) of the Nx components enlarges or diminishes relative to the others, with concomitant increases or decreases in the relevant Fy connection. This is a **re-organizational** model, and the final brain, or machine **could be the same absolute size as before, but the interrelationships between its components altered** (B). Logically, one would expect some difference in the brains' total behavioural output, or repertoire.

Imagine yet a third model, in which we try to take into consideration the **differentiation and development** of the Nx components and Fy connections through time. This is a hierarchical, or neural ontogenetic model (C). It adds the dimension of behavioural feedback with social actors through time, dependant on neurogenesis. Natural selection must act on that too, particularly in social animals. **The "genes" might not change the final absolute size, or even the organization of components, but instead code somewhat differently than before for ontogenetic events**. That is, the brain's behaviour could change at different times also, and thus offer a number of targets for natural selection. It is in this connection that I find Freedman's work so interesting.

I have always been struck by Ross Ashby's book, "Design for a Brain" because it suggested that by changing the quantitative relationships between parts in a machine, one could change the behavioural output. Similarly, I have always been impressed with the genetically-based defect known as microcephaly, in which it is possible to produce a brain within ape-sized limits of absolute size, yet behavioural repertoires that are unquestionably human, sometimes including language.[17]

It is my belief that at different times, each of these three basic models of the brain were under natural selection during human evolution. The challenge is to attempt to glean their operation through time from the fossil hominid record, paleoneurology, and our ever-increasing knowledge from comparative neuroanatomy. It is timely to review briefly what paleoneurology offers: (1) evidence for increase in absolute brain size; (2) evidence of reorganization of components, e.g. diminution of the lateral extent of the primary visual striate cortex, and possibly, cerebral asymmetry or lateralization of function; (3) if postcranial remains were complete enough, some indication of relative brain size. These are the direct lines of evidence. The indirect evidence for brain evolution is based on the following: (1)musculoskeletal shifts to different locomotory patterns (such as bipedalism), or increased use of the hands for toolmaking, using, and carrying; (2) an enriched archaeological record of tools, evidence for hunting and gathering, meaning a richer behavioural repertoire; (3) an increase in postnatal dependency time, i.e., a human ontogentic developmental pattern.

These latter three aspects of indirect evidence are of course no less important than the direct evidence, but do require considerable caution in interpreting the

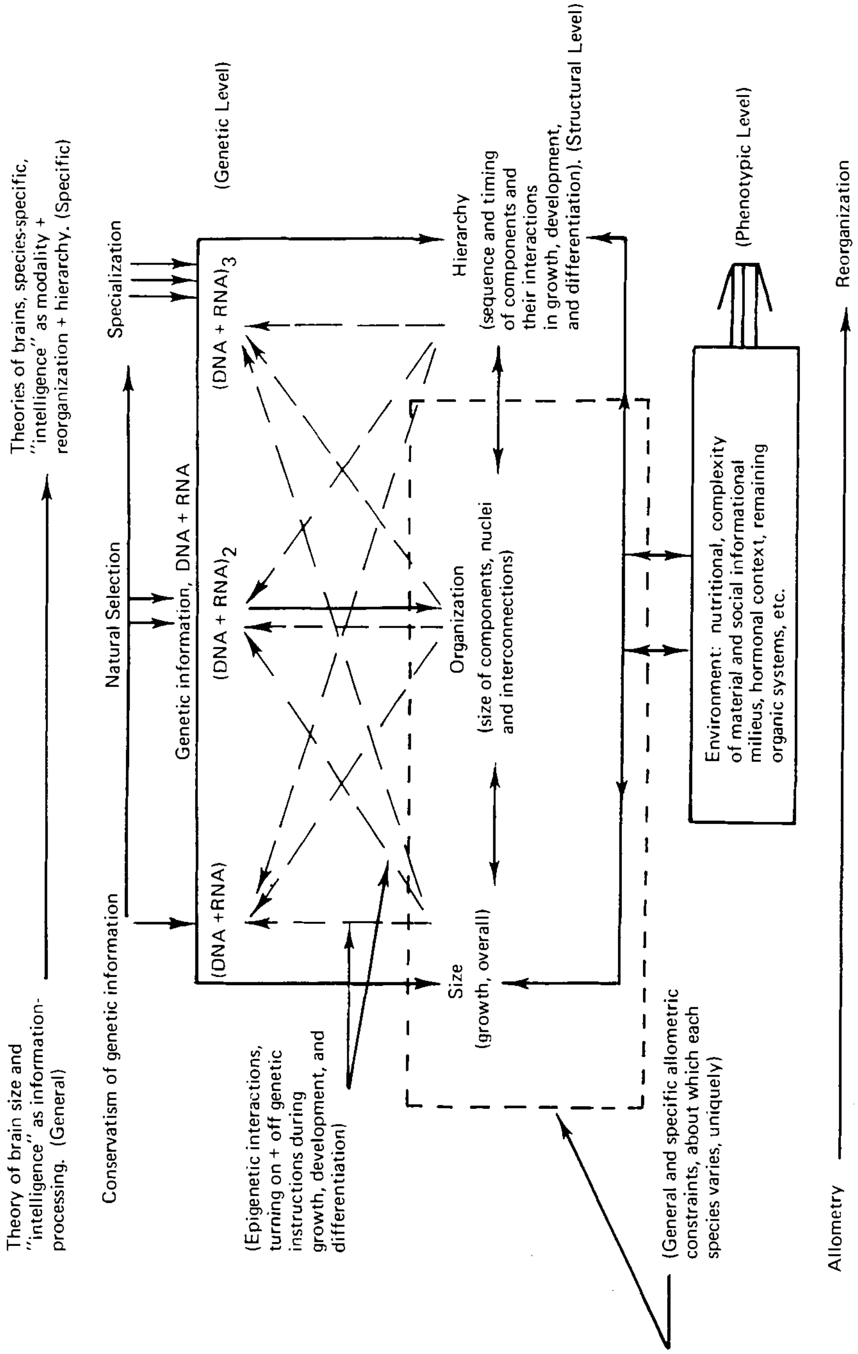


Figure 3. A model of how brain size (absolute), reorganization (differential sizes of components), and hierarchy might be conceived. The "Phenotypic Level" toward the bottom right portion of the diagram is almost exclusively regarded as brain size by most authors, but in this model is meant to include more than absolute size. For allometrists, only the left side appears to be of interest, the rest being "trivial." For anyone concerned about species-specific brain-behavioural evolution, i.e., *Homo sapiens*, the left portion cannot explain the totality that is the human brain (or any other animal's brain), as allometry is only the **constraint** around which other species vary, and brain size alone cannot be related to species-specific repertoires of behaviour, or unique evolutionary histories. This model **explicitly** regards the final phenotypic level as a complex orchestration between the neural events which unfold through the interaction of structural and regulatory genes, with natural selection operating upon at least three realms of genetic information. (This figure is adapted from Holloway 1979, where a fuller discussion can be found).

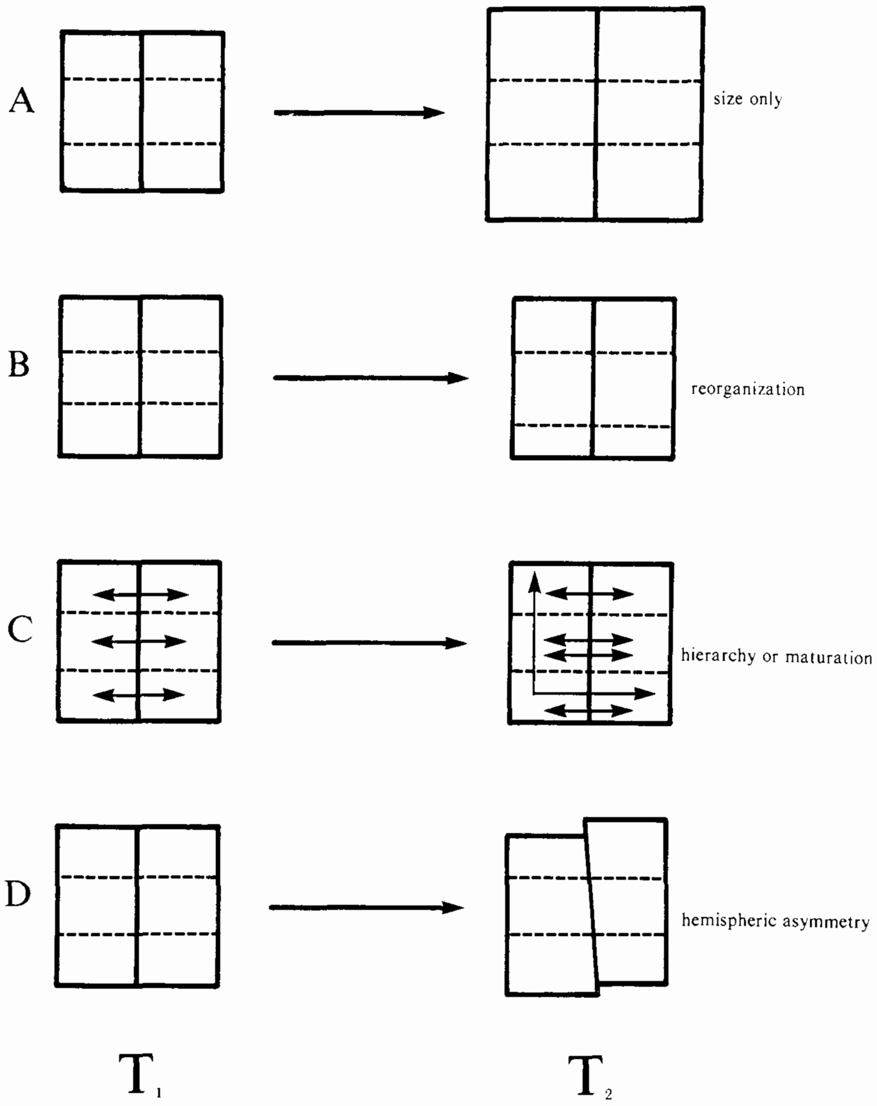


Figure 4. This figure shows four different possibilities of brain changes through time (T_1 to T_2). In **A**, the brain is shown with two hemispheres (left and right), and two transverse dotted lines which represent the central and lunate sulci respectively. The change from T_1 to T_2 is simply an increase in size (absolute) without any change between the size of components or connections between them. This change could occur isometrically or allometrically.

In **B**, the change from T_1 to T_2 does not involve any change in absolute brain size, but rather a change in components, such that the lunate sulcus is placed more posteriorly, thus expanding the posterior portion of parietal association cortex. This is a **reorganizational** model.

Model C depicts changes in **hierarchical** development without any change in absolute brain size from T_1 to T_2. The arrows represent fibre systems maturing at different rates and/or increasing in number between different cortical regions through the corpus callosum, although other brain structures and fibre systems could be involved.

In model **D**, absolute brain size remains the same from T_1 to T_2, but a more human-type of hemispheric asymmetrical petalial pattern has emerged (i.e., left-occipital, right frontal).

It is important to note that these four models do not exhaust the possibilities of brain changes through time when size, reorganization, or hierarchy are considered in different combinations. It is most probable that all four of these possibilities have been realized in human brain evolution at different times. Empirical paleoneurological evidence **does** exist for models A,B, and D, but model C can only be inferred from comparative neuroanatomy, although it must have lawful relationships with B and D. It is hopefully obvious that any plot of brain size vs. time ignores possibilities B,C, and D, each of which could have had very profound effects on cognition, social behaviour, and adaptation. Indeed, the shift from T_1 to T_2 in model B could represent a true case of "punctuated equilibrium," as could C or D. Model A could be interpreted as a "P.E.," but in fact might simply be due to a slight increase in body size, e.g., allometry.

dynamics of human evolution. For example, when the bony postcranial remains of *Australopithecus afarensis* show clear evidence of musculoskeletal patterns indicative of bipedal locomotion (corroborated by Dr. Mary Leakey's discoveries of footprints in the tuffs at Laetoli, Tanzania), one cannot leave the nervous system in a vacuum, but must accept the fact that some re-structuring of the nervous system had to have taken place to permit the operation of a new locomotory system. One will never be able to look at the surface of an endocast for *A. afarensis*, at the precentral gyrus, and say, "See, bipedal locomotion!" But one must accept that the brain was somehow **reorganized** to accomplish the locomotory tasks, and **all that that implies in terms of adaptive behaviour**. That is, locomotory behaviour could not evolve in either a behavioural **or** brain-structure vacuum.

Stone tools, made to more or less standardized patterns, do not appear in the fossil record until ca. 2 mya. This is almost 2 my after *A. afarensis*. Perhaps wood, bone, and even stones were used in the interim, but one cannot prove it from the archaeological record as yet. Either late, more advanced versions of *australopithecus* or early true *Homo*, perhaps *habilis*, were responsible for the known stone tools from Omo, Ethiopia; Lake Turkana, Kenya; Olduvai Gorge, Tanzania; and both Sterkfontein and Swartkrans in South Africa.[18]

These artifacts show a consciousness that we identify as "human," as they indicate some operation of socially derived and transmitted sets of social consensus, or "rules." For some of us, the making of stone tools to standardized patterns suggests language was present (Holloway 1969, 1976a, b, 1981). For others it does not, as they see pongids (particularly the chimpanzees) capable of the same tasks. But more to the point, I believe these fabrications provide the earliest clues to the intellect of these early hominids and, moreover, suggest probable refinements in brain structures mediating fine manipulative capabilities, and the use of planning or foresight, and application of the tools to a number of functions involved in subsistence.

Again, one cannot look at an endocast and say, "See, this bump for the thumb on the precentral gyrus indicates tool-making," or, "Notice Broca's cap, and how it must signal that these beasts had language!" Indeed, the KNM-ER 1470 and 3732 endocasts, from Lake Turkana, Kenya, at about 1.8 mya, do have a protruding left Broca's cap, and that is corroborative, but only that.

Lastly, the dental evidence has suggested a developmental pattern of eruption that is human and not pongid-like, in the Australopithecines (Mann 1975). We cannnot know for certain the duration of growth and postnatal dependence times, but it seems most reasonable to interpolate between our own extended times and the shorter times of our closest living relative, the chimpanzee. The point I am trying to make is that natural selection had a long and complex interface of socially-nourished relationships between offspring and adults to work upon in the course of hominid evolution, and those variations in development and differentiation of the nervous system underlying those social relationships are not empirically visible (as yet) to anyone working on endocasts, and may or may not have been reflected as increases in brain size or organization of the brain.

In sum, brain size increase, both absolute and relative, were probably interspersed with evolutionary episodes of reorganization of the brain, and subtle shifts in hierarchical ontogenetic unfoldings of the complex DNA-RNA symphonic movements that are essentially constant for all mammals, but in which minor variations on the themes become the basis for species-specific behaviour patterns and brain evolutionary changes.

POSTSCRIPT

Since the preparation of this paper, newer discoveries and hypotheses regarding brain evolution have been published which require comment:

(1) In the 52nd annual James Arthur Lecture (1982) R. D. Martin has examined the issue of how big brains can be supported metabolically, and has underlined the fact that basic metabolic rate and body size, when plotted in log-log style, show a slope of 3/4 (See also Martin 1981, 1982). As Holloway and Post (1982) indicated, brain size vs. body size allometric equations vary considerably depending on the taxa chosen. While Jerison's (1973) slope of .66 is most often used, the fact is that using all primates (N=89) including *Homo*, provides a slope of .78. If *Homo* is omitted, the slope is .76 (N=88). Pongids (N=7) give a slope of .58 and Old World monkeys (N=36), a slope of .57. As we indicated on our paper, the empirical evidence does not suggest any one **single** causal explanation appropriate to all taxonomic groups. For some, the relationship between brain and body size could be related to metabolic constraints (per Martin's suggestion). In other taxa, the classical surface area-volume relationship of .66 might have been the constraint. I believe Martin's hypothesis linking large brains, metabolic demands, and a K-selective environment, i.e., "stable," is an important conceptual contribution, and one that underlines the important issues of postnatal growth and dependency, as a target for natural selection pressures in the past, as I have so often suggested.

(2) The question of cerebral asymmetries has taken on a new and provocative twist. **Not only** does the female of our species have a larger amount of corpus callosum relative to brain size than the male (de-LaCoste-Utamsing and Holloway, 1982), **but** also, this difference appears early in the prenatal embryo. Statistically significant differences are observed in the dorsoventral width of the splenium and in the ratio of corpus callosal area/brain weight in fetuses of 26-41 gestational weeks, the differences favouring the female (Baack, et al. 1982). It should be recalled that it is the splenium of the corpus callosum that contains much of the interhemispheric transfer fibres connecting the two parietal lobes. These observations, if replicated with larger samples, would corroborate: (1) much clinical data regarding differential impairment and recovery rates in females suffering cerebral insults; (2) purported gender differences in symbolic-analytic and spatiovisual-holistic task performance; (3) observations

of greater degrees of cerebral asymmetries, both functional and structural, in males. Aside from replication studies being necessary, these data suggest two important tasks: (1) extending the studies to other primates (particularly *Pan* and *Macaca)* to see if this is only a human phenomenon; (2) to integrate this data in an evolutionary context as per Holloway 1981, (Holloway and LaCoste-Larymondie 1982). This author would be amazed if sexual dimorphism in cognitive and manual skills were **not** a target for past selection pressures.

(3) The Hadar A. L. 162-28 specimen preserves a posterior portion of the cranium from which a partial endocast has been made by this author. The internal table of bone was relatively intact, and some convolutional details are visible. While my studies are in a preliminary phase, I do not detect any pattern typical of *Pan*, suggesting rather, that by 3.5 mya reorganization of cerebral cortex had occurred prior to either absolute or possibly relative brain size increase. In fact, linear arc and chord measurements, taken on the Hadar specimen and those of five chimpanzee brain casts, strongly suggest that the interparietal sulcus extends further posteriorly to a more *Homo*-like position. An alternative hypothesis was tested, i.e., that the groove was a remnant of the lateral calcarine sulcus rather than the interparietal. This hypothesis is refuted by the measurements taken from the midline to the groove. The groove is too medially placed to be a lateral calcarine groove. A third alternative, to regard the Hadar morphology as unique, sharing neither *Pan* nor *Homo* characteristics is obviously a possibility, but there is no way in which such a hypothesis could be tested without a fuller record of *Pan* brain evolution during Miocene-Pliocene times. Such evidence simply does not exist.

(4) In a most recent text, Passingham (1982) maintains that the major differences between human and other primate brains are allometric. This position apparently is endorsed by Eldredge and Tattersall (1982) and McHenry (1982). In his text, Passingham refers to my 1979 article, but dismisses the examples of departure from allometric constraints on the basis of small sample size. Curiously, he uses one of the smallest samples (i.e., Shariff 1953) to try and prove an allometric relationship for sensory cortex, after criticizing my attempts to show the departures from allometry for *Homo sapiens*. If pages 67 to 78 (Holloway 1979) are read carefully it will be seen that yes, sample sizes were small but **four independent studies provided the same overall result**, i.e., that the primary visual striate cortex in *Homo* is less than expected for a primate of our brain size.

McHenry's (1982) review of "encephalization" is interesting. First of all, the review ignores Holloway and Post's (1982) caution about the "relativity of relative brain size," although McHenry is aware that the .67 exponent has been challenged by Martin (1981). More curious, however, are the estimated body weights for the Australopithecines, which have been critically discussed in Holloway (1976a, 1981a). Once again it should be pointed out that when multiple regression is used on the actual thoracic and lumbar diameters (rather than averages) of McHenry's (1975) sample, three important things happen: (1) the residuals decrease, (2) the multiple R increases, and (3) the predicted body weights for Australopithecines (gracile and robust) are significantly less. If, in addition, one uses a .01 criterion for identifying outliers, the predicted values are even less. The effect is to lower body weights and thus increase relative brain size and thereby "encephalization". The increases do not move the australopithecines into the *Homo* range, but they do advance significantly over the pongids, i.e., *Pan*. This is not to be taken as an endorsement of McHenry's methods utilizing modern *Homo* and pongid thoracic 12 and lumbar 5 vertebrae, although I believe McHenry's study to be of great value and hopefully refined and replicated with a larger and more diverse data base. The conclusion reached is that brain size remained small for a considerable period of time, which is not in dispute. But there are tantalizing bits and pieces of evidence which suggest that more than brain size was involved (e.g., cerebral asymmetry, expansion of parietal association cortex, and possibly in the Hadar 162-28 specimen, a true hominid, disposition of the lunate sulcus). I simply regard it as premature to label this period of early hominid evolution as one of stasis based on one phenotypic manifestation i.e., absolute brain size. It is far more probable that as our fossil hominid sample increases, we will discover "mosaics" within the mosaic of the evolution of the brain. The possibility of strong and rapid selection pressures for organization could make true punctuated equilibria in brain evolution which would not appear in size vs. time plots. Selection for increased relative brain size could be gradual and appear as a punctuated equilibrium blip in such a plot. Strong selection pressures for increased body size, which in itself could be gradualistic, might result in a curve showing a punctuated equilibrium change in slope. An apparent stasis on a brain size vs. time plot could include a radical shift to cerebral asymmetry and a truly "punctuated equilibrium" in cognitive skills. The point should be obvious: beware single-variable-time curves, particularly when the variable (such as brain size) is the most distal expression of a complex unfolding of genetic-environmental interaction about which we remain curiously ignorant.

NOTES

1. This paper is a revised, updated and expanded version of an earlier paper entitled "Phenotyptic windows other than size in the evolution of the human brain," presented at the Tenth International Congress on the Unity of the Sciences, November 1981.

2. I emphasize "normal" in this challenge, purposefully ignoring known abnormalities such as microcephaly, or the well-known effects of aging and alcoholism in reducing brain weight and particular abilities, of which "memory" is but one.

3. I am aware that the obverse is also true regarding brain components and developmental maturational events. Clearly, something else than absolute size differentiates human from chimpanzee brains.

4. All earlier references to these discoveries can be found in volume 57 No. 4 of the *American Journal of Physical Anthropology*, (1982), which is devoted exclusively to these finds.

5. Those who believe allometry to be the saving empirical bulwark of evolutionary studies should carefully read the recent article ("Rethinking Allometry") by Smith (1980). I personally believe but cannot prove, that the wholesale application of allometry to all size considerations in every aspect of evolutionary biology, but human and non-human primates in particular, grossly oversimplifies the problems, and we thus lose much interesting complexity.

6. Please refer to references at the end of this paper. Passingham and I appear to view the quantitative evidence on primate brain structures very differently, as I have indicated in the "Postcript" to this paper. The newer data set provided by Stephan, et al. (1981) now includes some 40+ brain structures for 45 different primates, including *Homo sapiens*. It is impossible in this paper to go through the differences between **actual** and **expected** (allometrical) values of all of the various structures for *Homo*. Many follow a close approximation, such as the cerebellum, neocortex, septum, hippocampus, mesencephalon, etc. Other structures do not, such as the lateral geniculate, visual striate cortex, striatum, pineal, paleocortex, hypothalamus, amygdala, etc. As a full quantitative study of these departures is in preparation, it should be pointed out that viewing allometry as "constraint" rather than "law," is a useful initial distinction. The newer Stephan, et al. (1981) data confirms my 1979 findings of significant departures, particularly in the visual cortex, but in many other structures also.

7. Freedman's finding are generally unpopular among social scientists, particularly anthropologists who believe all human groups have zero variance in genetically-mediated behavioural variation, but about 33% in serum protein variation. I find Freedman's work, despite all proper caveats about ethnic or racial labels, sample sizes, etc., exciting because it hopefully opens some additional "phenotypic" windows on attributes of neonatal behavioural variation, which surely must have some structural bias, if only temporarily manifested in neonates. This is, I believe, one example of hierarchical development, which I defined as follows in the 1979 article:

   "Hierarchy refers to the unique timing of embryological and all further ontogenetic development of brain processes; (that is, myelinization, neural nuclei, and fibre tract maturational interactions) and transactions with the rest of the organism and environment. It is essentially hierarchy that results in species-specific patters of maturation of different parts of the brain at different times in relationship to some ethological paradigm of infant-mature interaction (particularly in social animals)." (Holloway 1979: 62). Please refer to the original article for other examples.

8. There are no complete *A. africanus* endocasts with both right and left sides intact, including both frontal and posterior portions. It would have been much more fortunate if our early hominid ancestors had died standing on their heads, rather than choosing sides....The *A. robustus* specimens (SK1585 and OH5) are more complete, and suggest the human petalial configuration. In our analysis, all small-brained hominids were included together, which includes KNM-ER 1805 and 1813 from Lake Turkana, Kenya. We are not certain these latter two specimens are *A. africanus*. Nor is it so easy simply to assign them to *Homo habilis*, since they are quite different from the OH7 of Tanzania which was the type specimen for this taxon.

9. It should be obvious that any cerebral convolutional detail is dependent on the impressions the gyri and sulci make upon the internal table of bone of the cranium, through the three meningeal layers. The fossil hominids from Africa are quite variable in this regard. Almost all of the E. African hominids from Lake Turkana show zero relief, due mainly to their eroded condition. The Olduvai Gorge, Tanzania, specimens tend to be better preserved, but more incomplete. Suprisingly, the best examples are from South African sites. The Hadar, Ethiopian adult (AL 333-145) specimen of *A. afarensis* is, for the most part poorly preserved with regard to the internal table. However, even intact extinct crania of modern *H. sapiens*, and the pongids, tend to show very few reliable sulcal patterns. This does not render paleoneurology useless, but it does mean that the opportunities to trace convolutional patterns in hominids is rare, and must be done with great care, utilizing measurements wherever possible to test alternative hypotheses regarding the identification of any one sulcus, i.e., the lunate, interparietal, lateral calcarine, etc.

10. See Holloway (1980) for a discussion of a possible allometric relationship, and newer data on Spy I and Spy II. Stereoplotting studies to date show no evidence of my significant regional shape differences between neandertals and modern *Homo* endocasts, except for some dorsal platycephaly.

11. The Hadar, Ethiopian hominids assigned to the taxon *Australopithecus afarensis* have a high degree of sexual dimorphism in body size, to judge from their postcranial remains. One estimate goes as far as 145 pounds, others around 75 pounds. Such variability, not only phenotypically but also in terms of estimate procedures, and the lack of clear association between individual's crania and limb bone fragments makes accurate estimate of relative brain size impossible. This fact notwithstanding, I find it amazing that McHenry (1982) is willing to use a 415 ml estimate from Johanson and Edey (1980) to provide a relative brain size for this taxon.

12. Actually, her placement of this sulcus is in a *cercopithecoid* rather than a *pongid* position, and Falk (1980) offers no quantitative justification for placing it where she does. McHenry's (1982) comments regarding Dart's mistakenly identifying the lunate as the lambdoid suture are inaccurate, as it was Schepers who made that error. While McHenry cites LeGros Clark's (1947) classic paper, it would appear that he read it as carelessly as did Falk (1980).

13. I am aware of the controversies over the interpretation of whether or not this cortex is purely "associative" or in fact a secondary integrative sensory area. My use of the term "associative" is meant to be more in accord with the latter interpretation.

14. In particular, see LeMay (1976).

15. I am assuming that these works are so well-known that citation is not necessary. To indicate adequately all of the relevant publications in this area of neurobiology would simply take too much space.

16. In fact, both the Hadar AL 333-45 adult, and the AL 162-28 specimens show very slight left occipital petalias. In the former case, there is some post-mortem damage and distortion which could play a role in the petalial information, thus my hesitation to emphasize such a finding. The latter example is very indistinct.

17. I am referring to *Microcephaly vera*, but am very aware of the inherent difficulties in utilizing pathological examples in any evolutionary context. The point is very simple, however; certain cases of microcephaly demonstrate the possibility of "nature" constructing a brain-machine lacking in size, but retaining species-specific repertoires of behaviour in base components.

18. I am aware from Professor Isaac's demonstration and slides shown during this symposium, that simply bashing two rocks together produces very useful and acceptable cutting tools. But all of the sites I mention **also** contain forms made to **standardized** patterns. Either early hominids went to far more trouble than necessary to do their tasks, or these standardized forms hopefully provide clues to cognitive patterns and communicative exchanges more complex than in other animals. (See Holloway 1969, 1981a, for a fuller discussion).

19. Language cannot be proven simply by indicating a pronounced Broca's cap, or a bulging 3rd inferior frontal convolution. But when such a pattern appears together with an expanded inferior

parietal lobule, and stone tools made to standardized patterns, the corroborative evidence becomes more additive.

REFERENCES CITED

Asby, W.R.
1952 Design for a Brain. New York: John Wiley.

Baack, J., C. de Lacoste-Utamsing and D.J. Woodward
1982 Sexual dimorphism in human fetal corpora callosa. Neuroscience Abstracts.

Broom, R., and G.W.H. Schepers
1946 The South African Fossil Ape-Man. Pretoria: Transvaal Museum Memoirs 2.

Clark, W.E. LeGros
1947 Observations on the anatomy of the fossil *Australopithecinae*. Journal of Anatomy 81: 300-333.

Dart, R.
1925 *Australopithecus africanus*: the man ape of South Africa. Nature 115: 195-199.

1956 The relationship of brain size and brain pattern to human status. South African Journal of Medical Science 21: 23-45.

De LaCoste-Utamsing, M.C. and R.L.Holloway
1982 Sexual dimorphism in the human corpus callosum. Science 216: 1431-1432.

Eldredge, N. and I. Tattersall
1982 The Myths of Evolution. New York: Columbia University Press.

Falk, D.
1980 A reanalysis of the South African Australopithecine natural endocasts. American Journal of Physical Anthropology 53: 525-539.

Farquhar, M.N., K.J. Kosky and G.S. Omenn
1979 Gene expression in brain. In Bowden, D.M. (ed.), Aging in Non-human Primates. Pp. 579-600. New York: Van Nostrand Reinhold Co.

Freedman, D.G., and M.M. DeBoer
1979 Biological and cultural differences in early child development. Annual Review of Anthropology 8: 579-600.

Holloway, R.L.
1967 The evolution of the human brain; some notes toward a synthesis between neural structure and the evolution of complex behavior. General Systems 12: 3-19.

1969 Culture: a human domain. Current Anthropology 10: 395-412.

1969 Some questions on parameters of neural evolution in primates. Annals of the New York Academy of Science 167: 332-340.

1972 Australopithecine endocasts, brain evolution in the Hominoidea and a model of hominid evolution. *In* R. Tuttle (ed.), The Functional and Evolutionary Biology of Primates. Pp. 185-204. Chicago: Aldine.

1975 The Role of Human Social Behavior in the Evolution of the Brain. 43rd James Arthur Lecture at American Museum of Natural History, 1973. New York: American Museum of Natural History.

1976a Paleoneurological evidence for language origins. *In*: Origins and Evolution of Language and Speech. Annals of the New York Academy of Sciences 280: 330-348.

1976b Some problems of Hominid brain endocast reconstruction, allometry, and neural reorganization. *In*: Colloqium VI of the IX Congress of the Union Internationale des Sciences Prehistoriques et Protohistoriques. Pp. 69-119.

1978a The relevance of endocasts for studying primate brain evolution. *In*: C.R. Noback (ed.), Sensory Systems in Primates. Pp. 181-200. New York: Plenum Press.

1978b Problems of brain endocast interpretation and African Hominid evolution. *In*: C.J. Jolly (ed.), Early Hominids of Africa. Pp. 379-401. London: Duckworth.

1979 Brain size, allometry, and reorganization: toward a synthesis. *In*: M.E. Hahn, C. Jensen, and B.C. Dudek (Eds.), Development and Evolution of Brain Size: Behavioral Implications. Pp. 59-88. New York: Academic Press.

1981a Cultural symbols and brain evolution: a synthesis. Dialectical Anthropology 5: 287-303.

1981b Exploring the dorsal surface of Hominoid brain endocasts by stereoplotter and discriminant analysis. Philosophical Transactions of the Royal Society (London) B292: 155-166.

1981c Volumetric determinations on recent hominid endocasts: Spy I and II, Djebel Throud I, and the Salé *Homo erectus* specimen, with some notes on Neanderthal brain size. American Journal of Physical Anthropology 55: 385-394.

1981d Revisiting the South African *Australopithecus* endocasts: results of stereoplotting the lunate sulcus. American Journal of Physical Anthropology 56: 43-58.

Holloway, R.L. and M.C. De LaCoste-Lareymondie
1982 Brain endocast asymmetry in Pongids and Hominids: some preliminary findings on the paleontology of cerebral dominance. American Journal of Physial Anthropology 58: 108-110.

Holloway, R.L. and D.G. Post
1982 The relativity of relative brain measures and hominid mosaic evolution. *In*: E. Armstrong and D. Falk (eds.), Primate Brain Evolution: Methods and Concepts. Pp. 57-76. New York: Plenum Press.

Jerison, H.J.
1973 Evolution of the Brain and Intelligence. New York: Academic Press.

Johanson, D.C., M. Taieb and Y. Coppens
1982 Pliocene hominids from the Hadar formation, Ethiopia (1973-1977): Stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics. American Journal of Physical Anthropology 57: 373-402.

LeMay, M.
1976 Morphological cerebral asymmetries of modern man, fossil man, and nonhuman primates. Annals of the New York Academy of Science 280: 349-366.

LeMay, M. and A. Culebras
1972 Human brain-morphologic differences in the hemispheres demonstrable by carotid arteriography. The New England Journal of Medicine 287: 168-170.

LeMay, M. and N. Geschwind
1975 Hemispheric differences in the brains of great apes. Brain, Behavior and Evolution 11: 48-52.

LeMay, M., M.S. Billig and N. Geschwind
N.D. Asymmetries of the brains and skulls of non-human primates. *In*: Armstrong, E., and D. Falk (Eds.). Primate Evolution: Methods and Concepts. Pp. 263-278. New York: Plenum Press.

Mann, A.E.
1975 Some Paleodemographic aspects of the South African Australopithecines. University of Pennsylvania Publications in Anthropology No. 1.

Martin, R.D.
1981 Relative brain size and basal metabolic rate in terrestrial vertebrates. Nature 293: 57-60.

1982 Allometric approaches to the evolution of the primate nervous system. *In*: Armstrong, E., and Falk, D. (Eds.). Primate Brain Evolution: Methods and Concepts. Pp. 39-56. New York: Plenum Press.

McHenry, H.M.
1975 Fossil hominid body weight and brain size. Nature 254: 686-688.

1982 The pattern of human evolution: studies on bipedalism, mastication, and encephalization. Annual Review of Anthropology 11: 151-173.

Passingham, R.E.
1973 Anatomical differences between the cortex of man and other primates. Brain, Behavior and Evolution 7: 337-359.

1982 The Human Primate. Oxford: W.H. Freeman and Company.

Passingham, R.E. and G. Ettlinger
1973 A comparison of cortical functions in man and other primates. International Review of Neuro-biology 16: 233-299.

Smith, R.J.
1980 Rethinking allometry. Journal Theoretical Biology 87: 97-112.

Stephan, H., H. Frahm and G. Baron
1981 New and revised data on volumes of brain structures in Insectivores and Primates. Folia Primatologia 35: 1-29.

Tobias, P.V.
1967 Olduvai Gorge. The Cranium and Maxillary Dentition of *Australopithecus* (*Zinjanthropus*) *boisei*. Vol. 2. Cambridge: Cambridge University Press.

Question Period IV

Cooke: Thank you very much Dr. Holloway. We now invite members of the audience to ask any questions they may have about the human brain and about Ralph Holloway's talk. I'm very interested in the corpus collosum in the female because I've always felt that lateral thinking was largely a female's prerogative. Your question?

Question: That's what my question relates to, the corpus collosum being larger and different in the female. I've always thought that women's intuition is just quicker thinking in a woman's brain, more interconnections and seeing relationships between things that other people, men especially, can't notice. And I wonder if the development of the corpus collosum might be some evidence for more interconnections, quicker interconnection in different areas of the brain. And would that also be related to creative intelligence? I think creative and greater intelligence is somehow related to quicker chemical impulses in the brain, or something like that.

Holloway: Well one of the things I knew I was going to get into, and she knew she was going to get into, are the sexist aspects of this research. There's no way out of it, though. I mean those differences are there. To my mind, I am quite "sexist." I regard the human female brain as superior to the males'. I think they're better capable of holistic judgements and integrating complex symbolic aspects within emotional milieus. I think men are basically mechanical "children," children that are interested in mechanical toys. One of the things that I think is involved in this difference however, and I didn't mention it in my paper, is that all these asymmetries that we find in the hominid endocasts, and this business with the increase in the posterior fibres for the female, means that I regard spatio-visual integration as very important in hominid evolution. And I think that throwing behaviour, that is, where the movement of an object is calculated in the future, and the body is geared to throw, both with force and hopefully tremendous accuracy. A computed trajectory in advance to this really requires some brain reorganization. I think that's basically what is reflected phylogenetically in terms of the male brain. I do believe males are better throwers than females. But I'll tell you something else about this work. The sample size is fairly small but it"s highly significant at the present moment. She's gone back now and traced it in fetal brains and it does appear at about age 26 weeks. So it's there. How it got there, I leave to your imagination, but it is not culturally induced. I suggest it was evolutionarily induced.

(Professor Henry Higgins — reference: Shaw, G.B., "Pygmalion,"would have made the following observation on the above discussion: "The greater number of connections across the female corpus callosum probably leads to greater confusion between the cerebral hemispheres which accounts for women's illogical behaviour, inconsistency of approach and inability to make up their minds"- Editor).

Cooke: Thank you. Are there any other questions?

Question: First of all I'd like to congratulate both of you for your refusal to be intimidated by the micro people. I wanted to ask Dr. Holloway if he would comment on Dr. Tobias' interpretation of the *Homo habilis* endocast, mainly that the Broca and Wernicke's areas have been significantly enlarged in these specimens over the *Australopithecus* level?

Holloway: Yes, I think I can a little bit. It all depends on what Phillip is really saying is *Homo habilis*. This we haven't gotten out on the table yet. The endocast from Olduvai Gorge, I'm talking about OH-24, ...Twiggy...which is what Phillip showed, is the most rotten endocast in the world to tell you anything. The poor beast, I don't know if it happened during life, I think it was sat upon by an elephant. It was crushed in five layers and Ron Clarke did the most magnificent kind of reconstructive efforts to try and put that thing back together again but let me tell you, I can get nothing out of the endocast. OH-13, we didn't mention that. Is that a *Homo habilis*, or is that a beginning *Homo erectus*? It's somewhat a little later in time, the only thing we have is the posterior portion and I'm sorry to say I can't tell where Wernicke's area begins or ends. The 1470 endocast from Lake Turkana; almost no surface features whatsoever are available on it, but it does have a nice Broca's cap, but I couldn't tell you where Wernicke's area is on it. I don't even know if it's *Homo habilis*. We don't have its teeth. And when I put that 1470 through discriminate analysis, depending upon what groups I'm comparing it with, half the time it might be regarded as a robust Australopithecine and the other half of the time it might come out as *Homo erectus*. We need much more material than we've got. So Phillip will have to say how he comes to this. I think he comes to it on the basis of the fact that what our work is showing is that statistically you're finding different patterns here.

I'd like to mention something else if I can. On the Hadar adults, and on the infant, there is a marginal accessory sulcus, or vein. Now if you can remember some of your anatomy, the blood flows around the transverse sinus and then goes down to the jugular. This marginal sulcus comes down the side of the foramen magnum. There's only one other animal in which that is found and those are the robust australopithecines from South Africa, from Tanzania, and Kenya. I mean it's there in Olduvai Hominid-5, and you can find it in some of the Turkana material. And this is extremely interesting. And that's why his new date is so provocative, because here's a morphogenetic feature that is shared between the robust australopithecines and so-called *afarensis*. And maybe we didn't have to go from *Australopithecus afarensis* through *africanus* to get to *robustus*. I think the phylogeny is still all mucked up.

Cooke: Thank you Ralph. I don't think you need be unduly thrown by the adjustment of the dates. It's merely that the SHT tuff in the lower part of the section seems to be rather younger...likely to be younger than has been estimated. This doesn't change the dates in the upper part of the sequence.

Are there any other questions?

Question: There were two questions I might have asked you. The first one really concerns the shape of the brain in the parietal-occipital area. There are, I think, two ways it can develop. It can either develop from an outgrowth, if I had a sphere here, I could get a bump here by pushing out in that direction, I would now have a bump on top. That's the way you seem to visualize growth of the brain or growth of the shape. There is another possibility for growth of shape, and I'm not talking just about brains but about a limb or anything like that, that shape in fact is determined by resistance to growth, that is, I could get the lump out here by having a simple growth in this region, by restraining growth there and restraining growth here, now will the lump protrude. Now with respect to the parietal and occipital area that you were talking about, the growth of the brain, the shape of the brain, that region will be determined 1) by the intrinsic growth of the brain itself, which will develop a particular shape, and 2) by the resistance of the parietal and occipital bones and their sutures to the expansive growth of the brain. Now in the particular region in which you are investigating, of course you are getting a big change in that region with the attachment of the nuchal muscles and the development of that particular area. And the changes in the shape you are seeing are simply changes in the resistance to growth of the area.

Holloway: It's a possibility and it has to be explored, but I don't know the answer. I'm thinking of some recent synthesis that has been done on what are called cortical units of growth. These are the vertical columns that have been explicated so nicely by Szentagothai, Mountcastle, Vernon, and so forth in terms of ontogenetic growth and they have pretty well demonstrated that these...basic vertical units contain roughly the same number of nerve cells within them, between a wide variety of species. And what they're pointing out is that to get the differences in behaviour that one is talking about in these vertical units one has to worry about how they're interconnected. And I think it's those interconnections that make so much of the difference. But I must admit, I don't think that the nuchal musculature really offers resistance to the impression of let's say, the parietal over occipital lobe into the occipital brain. But it is a possibility. There really has not been clear-cut demonstrations of these kinds of mechanical factors that you're referring to in the growth. But if I were to take your position, I would say that there is enlargement and so forth which is impinging on the internal table of bone. And that's why we're able to see the changes, rather than your second proposal. But that's just my bias.

Question: The other question I had to ask, and again, not being an anatomist I get all my figures wrong, but I'm surprised you think that locomotive behaviour would have such a significant effect on the shape of the brain. I believe the figures, which again could be wildly wrong, are something like one million motor neurons in the human, and in the region of ten million sensory neurons, of which eight million, again I could have my figures wildly wrong, go to the eye. Now if you take the whole number of neurons in the brain which comes to about 3 or 5 orders of magnitude greater, let motor behaviour with just one million neurons, and of course the association areas in the brain, are really such a very small part, one would think, of brain function. If you look at the homunculus of the pre- and post-central gyrus, you know that particular one is limbs for example. And they hardly have anything there compared with the lips, and for example the fingers. Therefore, I would not have thought the locomotive behaviour could have such a great effect on brain shape.

Holloway: That's a fine question. I doubt that it does. From the endocranial casts I certainly can't tell anything. You know, what's missing from that whole discription are the unfolding myelogenetic events and so forth that take place in regions of the brain through time. They may be small in representation and so forth, but they are absolutely critical in the ontogenetic stages of development of an infant's behaviour.

Cooke: Are there any more questions? I've just one small one, you promised Ralph, that you were going to say why the impressions in the human brain endocast were so poor.

Holloway: I don't remember making that promise. I don't know the answer to it, Basil. I think it probably has to do with a combination of first, large brain size, secondly, sutures that remain open for a longer flexibility in the bones, and very, very thick meningeal tissues which surround the brain, particularly the dura mater. And I think it is just part of a conspiracy of nature's part really, to make certain that budding paleoneurologists have nothing to study.

Cooke: Well that's just one of our handicaps.

Some Archaeological Contributions Towards Understanding Human Evolution

GLYNN ISAAC
Department of Anthropology
University of California
BERKELEY, California 94720

After July 1, 1983:
Department of Anthropology
Peabody Museum
Harvard University
CAMBRIDGE, Massachusetts 02138

Abstract: Comparative studies of modern humans and of their close living relatives make it clear that during the course of evolution, humans have diverged from the apes even more in their behaviour and their mode of adaptation than in their gross anatomy. For some of the innovations that have occurred in the human line of descent, we can use archaeology to ascertain the sequence, position and date of those changes. Behavioural novelties that can be thus investigated include (1) the use of sharp edged tools, (2) the eating of meat from the carcasses of large mammals (3) the transport of food (meat) to particular places where concentrated patches of refuse formed. These behavioural shifts had occurred by two million years ago. That is, at the time of, or just before, the appearance of the first hominid forms with conspicuously enlarged brains (*Homo habilis*). The possible relationship of these shifts to selection pressures favouring greater skill, greater sociality and greater communicative ability thus becomes an important question for consideration and enquiry.

Résumé: L'étude comparative de l'homme moderne et de ses proches parents actuels démontre clairement que les traits évolutionnaires séparant l'homme du singe relèvent plus du domaine du comportement et du mode d'adaptation que du domaine de l'anatomie pure et simple. Grâce à l'archéologie certaines des innovations se rapportant aux ancêtres de l'homme peuvent être datées, ou du moins ordonnées. Les innovations dans le domaine du comportement incluent (1) l'utilisation d'outils tranchants, (2) la consomption de viande provenant de carcasses de grands mammifères, (3) le transport de la nourriture (viande) jusqu'à certains endroits où l'on retrouve des concentrations de déchets. Ces changements d'attitude avaient déjà pris place il y a deux millions d'années, soit à l'époque de, ou peut-être un peu avant, l'apparition des premiers hominides arborant un cerveau remarquablement développé (*Homo habilis*). La possibilité d'une connection entre ces changements d'attitude et les pressions exercées par la sélection naturelle favorisant une plus grande adresse, une vie sociale plus avancée, et de plus grands talents pour la communication doit être sérieusement considérée et étudiée.

Keywords: **Evolution, human behaviour, hunting, gathering, sharing sex-roles**

INTRODUCTION

There are two major approaches to inquiry into human evolution. One is to compare the characteristics of the species *Homo sapiens* with those of its close living relatives. Anatomy, physiology, biochemistry and behaviour can all usefully be considered and the comparisons serve to define what evolutionary differentiation has taken place.

The other major approach is to study the stratified record of the past. From paleontological, archaeological and paleo-environmental evidence, propositions can be tested about the sequence of stages through which the human condition has been derived.

Although those who study the fossil record often give the impression that this record is *the* major source of information about human evolution, this is surely not the case. Most of what we know about the evolutionary differentiation of organisms in general, including humans, comes from intelligent comparative studies. This is why, within 12 years of the publication of the *Origin of Species*, and before the recovery of any significant hominid fossils, Darwin was able to give an account of the *Descent of Man* that represents a fair first approximation of accounts that are still being presented today (see Pilbeam 1980, and Landau 1981 for discussion of aspects of this). However, the study of the record of the past, incomplete though it is, does make an important contribution by allowing the investigation of the sequence, context, and timing of some of the changes that have occurred. This information in turn can be woven into a narrative version of human evolution that can be used as a replacement for the origin myths that were a part of all human cultures before scientific evolutionary studies ever began. One of the species specific characteristics of *Homo sapiens* is a love of stories, so that narrative reports of human evolution are demanded by society and even tend toward a common form (Landau 1981).

The dominant role of comparative studies is particularly clear in the investigation of the evolution of human behaviour. The complexities of primate behaviour fossilize very poorly, whereas we have a wealth of data from living forms. The same is, of course, true for the even greater variability and complexity of human economic, social, cultural, and intellectual behaviour. However, there is a difference. During the course of human evolution, our ancestors began to be involved in some behaviours which do fossilize; they began to manufacture tools and equipment from durable substances such as stone; they began to include foodstuffs in their diet that leave a durable residue, notably meat wrapped round bone; and they began eventually to live in social groups that used particular bases of operations for enough time for middens to accumulate. These physical traces of past behaviour are the raw material of archaeological inquiry into past behavioural and cultural systems. Their existence in strata dating back to 2 mya (million years ago) or more gives archaeologists an important role in the study of human evolution that is complementary to that of the paleontologists who study the fragmentary bones of these toolmaking ancestors.

It is largely from comparative studies of human beings and their close living relatives that we derive our questions about the history of changes in behavioural and adaptive patterns. Table 1 sets out some of the major contrasts which such comparisons indicate as being important. Because of the complexity of higher primate behaviour, this list is necessarily simplistic; it is also selectively biased in favour of behavioural traits that seem potentially important to me as an archaeologist. However, while granting the simplicity and the bias, I do argue that this kind of list has served the useful heuristic purpose of focusing the attention of paleoanthropologists on a series of aspects of adaptive change that transcend both the technical features of ancient artifacts and the morphological details of fossil bones.

The items on the list must not be considered as isolated traits but as components in a complex series of interconnected behavioural, physiological and anatomical systems which together make up the distinctive, flexible mode of adaptation that characterizes our species. Let us assume for the moment that all or most of these points of contrast reflect innovations and modifications that have occurred during the course of human descent since divergence from the last common ancestor that we shared with any living ape species. What do we know about the sequence of evolutionary changes bringing about these differences? The fossil record shows clearly that major anatomical changes occurred in the following order:

1. shift to bipedal locomotion (by 4 mya),
2. initiation of a trend to brain enlargement (about 2-2.5 mya),
3. initiation of a trend to reduction in tooth and jaw size (about 2 mya),

TABLE 1

Selected Important Contrasts Between Humans and Their Closest Living Relatives, the African Apes. Italics Indicates That the Feature is Directly Detectable in the Fossil or Archaeological Record

Anatomical/Physiological contrasts	**Behavioural/Social contrasts**
• Modification for *bipedal locomotion* and stance	• Language and symbolic gestures
• Modified *hands*	• Use of *tools and equipment*
• *Enlarged* (reorganized) *brains*	• *Carrying* objects around
• Thick enameled *cheek teeth*	• *Central place foraging with home base*
• Concealed ovulation	• *Division of labour*
• Reduction in hair cover	• *More meat in diet* (from *larger prey forms*)
• Retarded maturation/prolonged dependency	• Male investment in child rearing
	• Marriage
	• Social systems based on reciprocity

4. loss of a marked degree of skeletal robusticity which characterized all early hominids until about 0.03-0.05 mya.

The question now arises, can we tell how the list of changes in behaviour relate to these anatomical shifts? Can we assess something of the evolutionary dynamics which may have wrought combined changes in behaviour and anatomy?

At present archaeology can contribute little or nothing to an understanding of the adoption of bipedal locomotion, but the oldest known artifacts, and the oldest known evidence of meat eating and the oldest known archaeological sites all derive from the same strata that contain the earliest known hominid fossils that show very marked non-allometric brain enlargement. There are thus good *a priori* reasons to expect that archaeology can be used to make critical tests of alternative hypotheses regarding the behavioural and adaptive systems that were associated with very early stages in the trend to brain enlargement. It is on this potential contribution by archaeology that this review is focused.

ARCHAEOLOGICAL EVIDENCE

Africa is the only continent which has so far yielded undoubted archaeological evidence which dates to the time range before 1.5 mya. Sites which are probably this old are known in northwestern Africa, East Africa and South Africa (Table 2) but so far it is only from eastern Africa that we have clear dating evidence and extensive investigation that relate to the questions treated in this review. Consequently, the review will concern itself predominantly with East Africa.

In this portion of the review, I will try to set out brief statements of the nature of the archaeological evidence that are as empirical and as free of interpretation as possible. In subsequent sections I will enter into discussion of alternative behavioural interpretations and the consequent implications regarding larger issues in human evolution.

The main classes of material evidence with which archaeologists are currently working consist of the following:

1. *Artifacts* - stones fractured by deliberate percussion (Figure 1);
2. *Cutmarks* - bones which have been marked by the slicing or scraping contact of sharp stone edges;
3. *Sites* - clusters of stone artifacts in small localized patches, sometimes with significant quantities of bone also present, sometimes with little or no bones;
4. *Paleogeographic distribution patterns* - the spatial configuration of artifacts, cutmarks and sites considered in relation to the distribution of water and to plant and animal communities.

These are the lines of evidence. Can they be used to elucidate significant aspects of early hominid adaptive systems?

TOWARDS TESTABLE INTERPRETATIONS

In the first round of research on early sites, archaeologists tended to interpret the evidence as having been formed largely as consequences of the familiar behaviour patterns of recent humans. It seemed intuitively obvious that the evidence indicated an adaptive pattern involving toolmaking, hunting and carrying food to "living sites" or "home bases," where it was presumably collectively consumed (e.g., Clark 1970, Isaac 1969, 1976, 1978; M.D. Leakey 1971 and many others). Although these interpretations may well prove to be valid, subsequently archaeologists began to recognize the need to consider a broader range of possible explanatory hypotheses. Emphasis in research shifted from simply defending and 'confirming' the explanation that had at first sight seemed most plausible, to deliberately thinking up sets of feasible multiple alternative hypotheses. Each such rival hypothesis tends to carry contrasting expectations with regard to the detailed configuration of evidence, so that research has become the classic cycle of *hypothesis formulation* to *deduction* and *prediction* to *observation* to *hypothesis rejection or revision* and so on. In practice, in order to determine the test implications of different hypotheses, it has often proven necessary to engage either in *experimental studies* of process, or in observational studies of the differential effects of various *natural processes*.

This kind of work began among paleontological researchers such as Brain (1967, 1976, 1981), Behrensmeyer (1975), Hill (1975) and several others. It became a part of the approach of people working on the Olduvai materials with Mary Leakey's help and encouragement (Jones 1981, Potts 1982, Bunn 1982), and in the form of a team effort supported by the NSF in 1977 it became an organised research effort of the Koobi Fora Research Project (Isaac 1977, 1981, Bunn, et al. 1980). Recently, the whole issue of the need to consider alternative explanations has been brought dramatically to general attention by Binford's book *Bones: Ancient Men and Modern Myths* (1981). Among the Koobi Fora research group, enquiry into the behavioural meaning of the archaeological evidence began in 1977 to be formulated as a series of questions. Tackling some of these questions has involved very explicit multiple alternative hypotheses, while others call for more exploratory kinds of investigation. This review can only briefly introduce the lines of inquiry and provide references to more detailed accounts.

1) How were early stone tools made and what role did they play in adaptation?

Relevant work has been undertaken by N. Toth (1982) at Koobi Fora, with comparable studies at Olduvai by P. Jones (1979, 1981). Both Toth and Jones have shown that the characteristics of raw materials used have marked effects on artifact forms. Independent experiments by both have shown that the early tools can perfectly well be used to accomplish a wide range of tasks — notably cutting up animals, including the largest pachyderms, chopping off

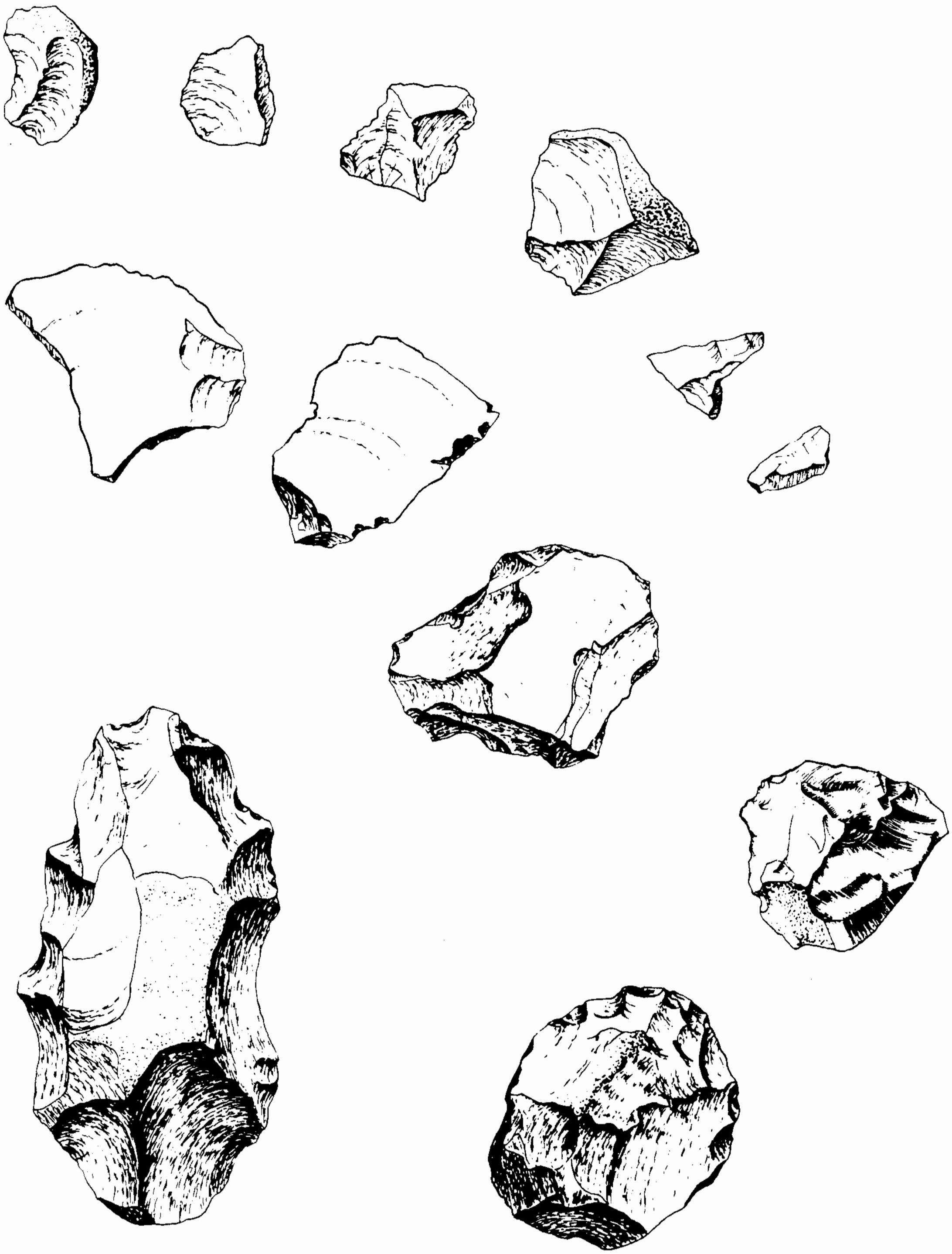


Figure 1. A representative array of sharp-edged stone artifacts from a 1.5–2.0 mya site. The 8 pieces in the upper left sector are flakes and flake fragments which are knife-like objects. The lower right items are stones from which flakes have been struck, that is cores/core tools. The larger item at lower left is a so-called Karari scraper—which may well be simply a neatly executed source of flakes—a fancy core form. Flakes normally outnumber cores and core tools 20 to 1.

TABLE 2

	1.0-1.5 mya	**1.75-2 mya**	**>2 mya**
Eurasia[1]	Ubeidiya ?		
North Africa[2]	Ain Hanech ?		
	Casablanca ?		
East Africa[2]	Gadeb	Melka Kuntoure ?	Kada Gona (?2.6)[5]
	Melka Kuntoure[3]	Koobi Fora (KBS)	Omo Shungura F. (2.1)
	Chesowanja[4]		
	Peninj		
	Olduvai Gorge		
South Africa[2]	Sterkfontein Mbr.5[6]	Swartkrans[7]	
	Swartkrans A		

Footnotes:

1. I regard Ubeidya in Israel as the only well established Eurasiatic archaeological site that may be of this age. Java has yielded fossils but no certain sites. Yuan Mou in South China is probably 0.7–1 mya. Also, Isernia in Italy.
2. See Clark, 1970 and Isaac, 1981 for summaries and reviews with references.
3. Melka Kuntoure, see Chavaillon et al, 1979.
4. Chesowanja, see Gowlett et al, 1981.
5. Kada Gona, the claimant for the oldest known sites has not been published in detail and must be regarded as uncertain until more is known (see Roche and Tiercellin 1977 and Harris in: Lewin 1981).
6. For Sterkfontein see Tobias and Hughes 1969, Stiles 1979.
7. Swarkrans, Brain has provided personal communication of kinds of artifacts in very early levels.

branches, whittling wood, cutting hide, bark, stems and fibres. Toth, working with L. Keeley, has gone on to seek evidence as to the tasks for which some of the tools actually were used. Using the fact that silicious rocks acquire different kinds of microscopically visible polishes when moved against different substances, Keeley and Toth (1981) showed that in a small sample from Koobi Fora four flakes had been used for cutting meat, two for whittling wood, and suprisingly that two had been used for cutting soft plant tissue, perhaps grass.

2) Is there clear cut evidence for hunting and/or meat eating by early hominids?

This enquiry has been pursued by R. Potts in an extensive reexamination of bone collections from the Olduvai sites (Potts and Shipman 1981, Potts 1982), and by H. Bunn working with bone collections from Koobi Fora and Olduvai (Bunn, et al. 1980, Bunn 1981, 1982).

These enquiries broke into two parts — first, are combined clusters of artifacts and bones evidence of food transport and of meat eating? This question in turn involves complex enquiry into how such clusters could have formed, and discussion of this issue is deferred. Second, is there evidence for meat eating independent of the spatial association of artifacts and bones? Both for Olduvai and Koobi Fora the answer turned out to be affirmative. Careful searching revealed numbers of bone specimens with distinct marks where sharp edged stone implements had cut or scraped against the bone surface while it was fresh. The position and characteristics of these marks strongly imply that stone tools were being used in the following operations:

a. dismemberment of carcasses by the severing of sinews and tendons at joints.
b. the removal of muscles from bone shafts.
c. the freeing of skin from bones which are surrounded by little or no muscle but which contain marrow (e.g., bovid cannon bones).

The sizes of animals on which cut marks were found range from small gazelles to giraffes, hippos and elephants. Cut marks were found on bones in clusters with artifacts (i.e. classic sites) and on bones found scattered in beds which also contain hominid bones but no detectable artifacts.

These findings appear to eliminate models of human evolution that do not allow for significant meat eating by the earliest known tool making hominids in the time range from 1.5 to 2 mya. These hominids were cutting up the meaty portions of animals far larger than any living non-human primate is known to feed on. However, the cut mark evidence leaves unsettled a number of questions: how frequent were such meat eating bouts? Was meat being acquired primarily by hunting or by scavenging dead carcasses or both? Were portions of carcasses transported to central locations for collective consumption?

These questions relate in turn to what has become the central and most debated issue in behavioural interpretation of the early archaeological remains. *How did the observed clusters of artifacts and bones form?* Are these clusters evidence of the transport of meat to central places for collective consumption? Or, put in more emotionally charged words, are these sites fossil 'home bases' to which food was carried and shared?

In relation to the latter question, we recognized back in 1977 that it was crucial that we conduct a series of tests which subjected our favourite hypothesis (Isaac 1969, 1976, 1978) to genuine jeopardy by comparing it with realistic alternatives. This is also the issue on which Binford's (1981) skepticism is correctly focused.

Figure 2 shows a series of rival hypotheses to account for the observed configuration. In our research we set about defining the distinguishing implications of each hypothesis and comparing them with observations on the materials and their configuration. Note that the various hypotheses are not mutually exclusive, so that interpretation winds up involving evaluation of the relative importance of various processes rather than simple Popperian falsification.

The results have been partially reported elsewhere (Bunn, et al. 1981, Isaac 1981, Isaac in press). They will only be very briefly indicated here.

The hydraulic jumble hypothesis has been evaluated through experimental research by Kathy Schick (in preparation) on the effects of river flow on artifacts and bones. It also can be checked by searches for pieces that fit back together. These can be expected only rarely in a purely hydraulic jumble, and when they do occur they should not form tight spatial clusters. Both these investigations indicate clearly that while they may have been mildly water disturbed, the best preserved combined clusters of artifacts and bones are not purely hydraulic jumbles.

Similarly, while there is good evidence for carnivore gnawing of bones there is equally good evidence from cut marks for hominid involvement in dismembering and meat removal. These would not be predicted had the hominids merely come to places where carnivores had accumulated bare bones simply to exploit marrow (cf. Binford 1981).

In summary, we have failed to eliminate the hypothesis that hominids actively detached at least some meat-encased bones from carcasses, and then transported these bones to places where many artifacts and other bones were accumulating. Whether this implies a 'base camp' or collective consumption (sharing) is much harder to judge. I will return to this point later.

Another member of the group, Ellen Kroll, has pursued the question: *are there regularities in the spatial configuration of objects within sites?* If so, can these be interpreted in terms of the behaviours of the tool makers who formed the sites (given that they are not purely hydraulic jumbles). The question and approach are discussed in Kroll and Isaac (in press). The research is still in progress.

LARGER SCALE MODELS OF HUMAN EVOLUTION

Figure 3 summarizes the novel behavioural elements that seem to be positively documented in the archaeological record. These can be arranged into a spectrum of different permutations and intensities. One extreme involves central place foraging and the other does not, with one being intermediate. The confirmed elements are:

a. Transport (carrying) of stones.
b. Stone tool making and using.
c. Meat cutting and dismemberment of carcasses (plus wood working and plant tissue cutting).
d. Transport of detached limbs and other body parts.
e. Concentration of transported stones and bones in some areas. Breakage for marrow extraction can occur.

Here the model branches:

f) Consumption by individuals in sheltered places away from other conspecifics (i.e., deliberate avoidance),

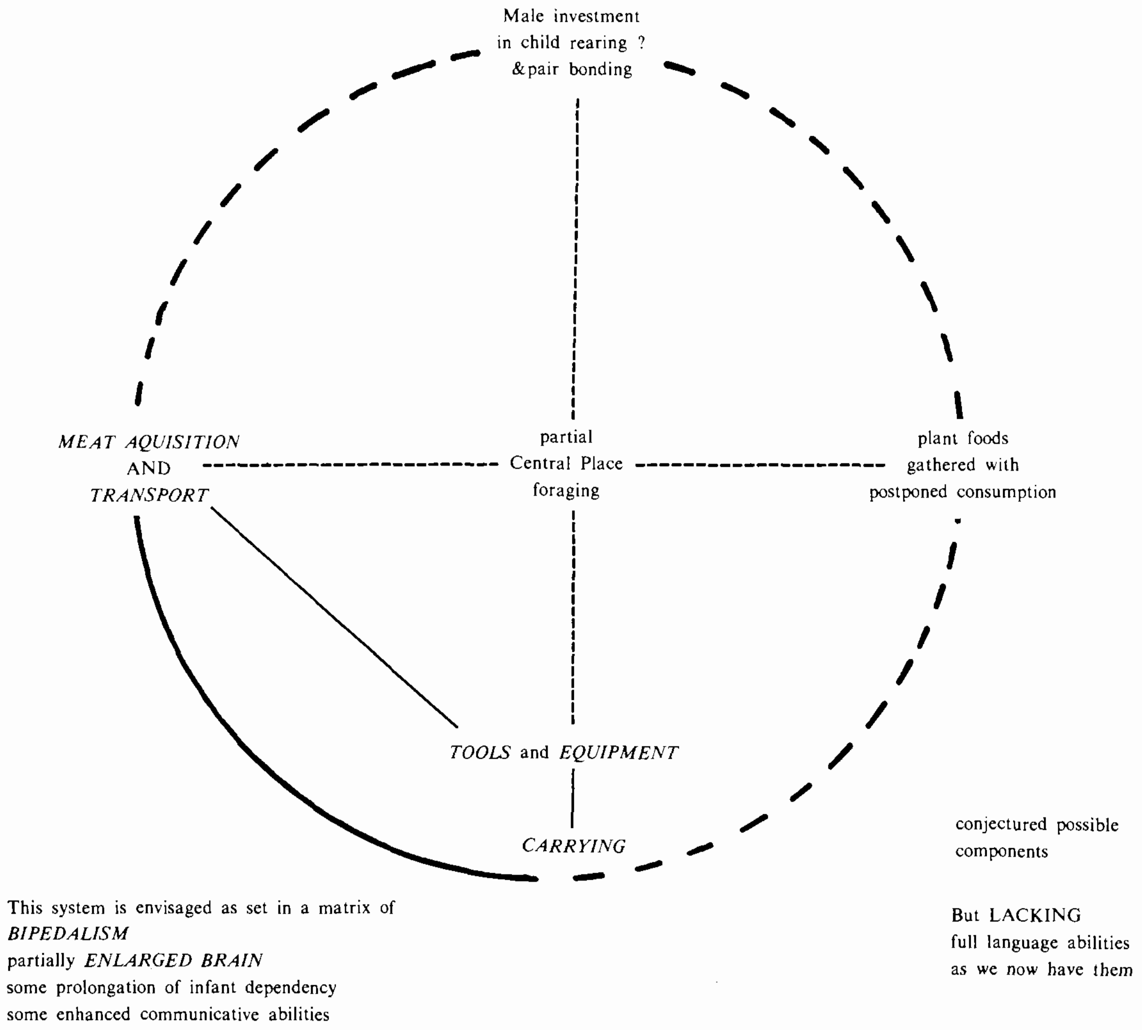


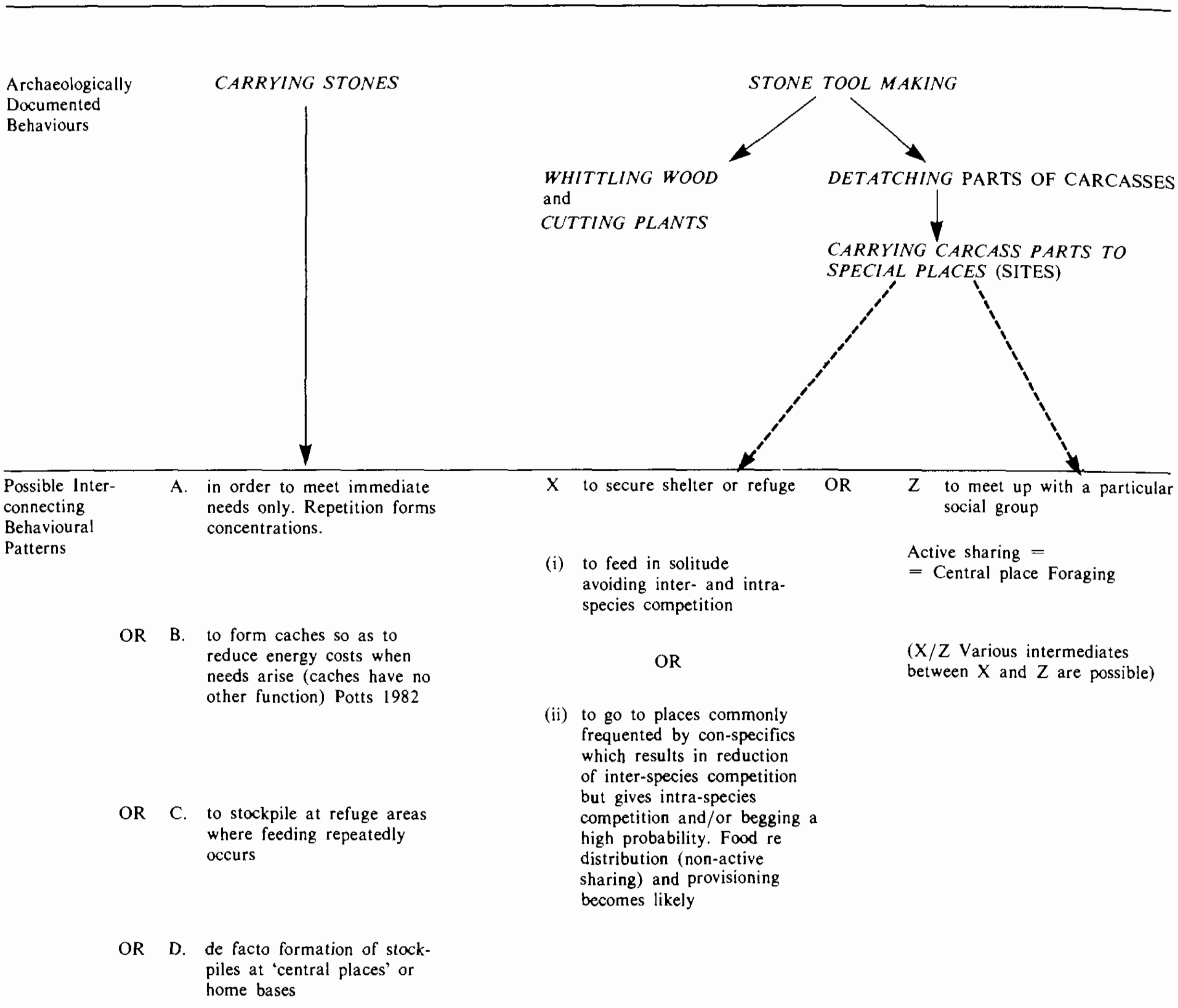
Figure 2. A possible configuration of behavioural elements for toolmaking hominids of 2 mya. The diagram intends to make a series of related hypotheses explicit. It does not purport to represent established fact. Elements for which there is direct archaeological evidence are shown in capitals, italicized and are linked with solid lines. Other potentially linked behaviours are shown in lower case and joined with broken lines. At some stage in human evolution these behaviours did become linked. The question is when?

f″) Consumption by individuals in sheltered places with other individuals crowding round and scrounging. Potts (1981) has also proposed for consideration that the sites might represent places where tool making stones were cached and to which parts of carcasses were carried (without involving sharing).

f‴) deliberate active sharing at particular places which functioned as socially defined 'central places.'

At present, we can not distinguish these clearly. I would expect that f′ would produce a highly dispersed scatter of cut marked and transported bones while f‴ would produce a tight cluster. Data currently available imply the existence of relatively tight clusters. Thus, I favour the retention of f″ or f‴ — that is to say we emerge with a working hypothesis that by 2 mya *some hominids were at least incipient central place foragers.*

This working hypothesis needs to be further tested and elucidated, but if it survives such additional testing, then I argue that it can be incorporated as an important component in establishing the selection pressures which led to the development of language abilities, planning abilities, and the ability to play social chess. (By social chess I mean the extraordinary human ability to envisage long-term concatenations of



social moves and counter-moves, and to be able to manipulate these). All these abilities are presumably the phenotypic qualities that led natural selection to favour genotypes that developed somewhat enlarged and reorganised brains.

Figure 3 suggests a structural model for innovations in behaviour that had begun to be established by 2 mya. The model need not imply that the tool-making, food-carrying hominids of this time were human. I am of the opinion that if we had specimens alive today we would find ourselves obliged to put them in the zoo, not in the drawing room or an academy!

Now the logic of a satisfying explanation for the development of human language ability requires not only that it explains the human condition, but that it makes intelligible the fact that chimpanzees and other higher primates do *not* have language. The insertion of this non-human central-place foraging-stage model fulfills this requirement. It suggests that savannah living resulted in the important differential of mobility between females and males. This in turn gave adaptive advantage to individuals involved in meat acquisition, provisioning and/or food sharing. Predictably, these selection pressures would have been absent or very much weaker for ancestral forest or woodland apes. It should be noted that Lovejoy (1981) has advanced the rival hypothesis that ancestral male hominids began provisioning their mates and young while the populations were still largely arboreal, non-bipedal and non-meat eaters. This is an interesting hypothesis, but because plant foods are so much less portable than meat, and because mobility is less crucial in woodlands, I find the suggestion less plausible (Isaac 1981).

In summary then, Table 3 suggests a scenario for the relation between behaviour and anatomy in human evolution.

TABLE 3

A Scenario of Behavioural Changes and Their Anatomical Manifestations. These Should be Understood as Propositions for Testing, Not as Established Facts

Stage 0 Last common ancestor of hominids and African apes:

- non-bipedal
- feed-as-you-go-foragers
- tool use absent or on a small scale
- meat-eating absent or on a small scale

Stage 1

- occupation of habitats with larger gaps between patches of trees
- adoption of bipedal gait in relation either to feeding posture (Pilbeam 1980, Rose 1976) or to travelling and carrying (Hewes 1961) but remaining part arboreal
- adoption of distinctive diet requiring 'megadont' masticatory apparatus

(Among these three innovations we can not at present distinguish sequence. These behavioural shifts are reflected also in the anatomy of the locomotor system and of the jaws.)

Stage 2

- become partially involved in central place foraging patterns (this could have begun to occur in Stage 1)
- intensified involvement with equipment to include the making of sharp edged stone forms (non-stone tool using may well have been a part of Stage 1)
- intensified meat-eating beyond the level of any non-human primate
- plant foods remain dominant in the diet
- an increase in male investment in child-rearing? This might have begun earlier (cf. Lovejoy 1981) or later

It can be argued that these changes place *positive* selection pressure on

- *communicative ability* and *social coalitions*
- prolonged infancy for learning communication, mechanical and social skills

and hence on *Brain enlargement* (400-500cc to 600-900cc) plus *negative* selection on jaw and tooth size

Stage 3

- consolidation through natural selection, including kin selection, of the distinctive human pattern:
- elaboration of the neurophysiological basis of language
- increase of tool/equipment dependency including the use of fire
- intensification of the central-place-foraging pattern, including active food-sharing
- formation of pair bonded reproductive units (if these did not exist already)
- development of kin-based social networks with reciprocal obligations
- elaboration of language and symbols

Stage 4 A final shift involving a great reduction in skeletal robusticity and a great surge in the rate of social/cultural differentiation and elaboration. (Perhaps this shift involved the competitive success of larger social coalitions, which in turn required more fine-tuned communication systems such as refined language and more elaborate symbols? *Plus* a suppression of anti-social, hormone mediated 'brute force' behaviours?).

TIMING

Stage 1 Must have gone through after the origin of the hominid clade, and before 4 mya. *A. afarensis* and *A. africanus* may well be fossil manifestations of this adaptive stage.

Stage 2 The symptoms of Stage 2 become evident around 2 mya in association with the oldest fossils of the genus *Homo* which in turn show the first clear evidence of brain expansion.

Stage 3 This presumably runs from about 1.5 mya with the appearance of *Homo erectus* and proceeded stepwise or gradually until about 100,000 years ago.

Stage 4 The loss-of-robusticity- transition is particularly conspicuous in the time range between 30,000 and 50,000 years ago, but it may have begun earlier.

The first important thing is not to look at this scenario as the 'truth' but to recognize that *it makes a series of propositions sufficiently explicit so that we can see the importance of finding ways to test them.* The second important thing is that it shows that archaeological tests of alternative hypotheses about behavioural shifts have a crucial role to play in improving our understanding of the last few million years of human evolution.

REFERENCES CITED

Behrensmeyer, A.K.
1975 The taphonomy and palaeoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolph, Kenya. Museum of Comparative Zoology, Bulletin 146:473-578.

Binford, L.R.
1981 Bones: Ancient Men and Modern Myths. New York: Academic Press.

Brain, C.K.
1967 Hottentot food remains and their meaning in the interpretation of fossil bone assemblages. Namib Desert Research Station, Scientific Papers 32:1-11.

1976 Some principles in the interpretation of bone accumulations associated with man. *In*: G. Ll. Isaac and E.R. McCown (eds.), Human Origins: Louis Leakey and the East African Evidence. Pp. 97-116. Menlo Park: W.A. Benjamin.

1981 The Hunters or the Hunted? Chicago: University of Chicago Press.

Bunn, H.T.
1981 Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. Nature 291:574-577.

1982 Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-Pleistocene Hominids in East Africa. Ph.D. Dissertation, Department of Anthropology, University of California, Berkeley.

Bunn, H.T., J.W.K. Harris, G.Ll. Isaac, Z. Kaufulu, E. Kroll, K. Schick, N. Toth and A.K. Behrensmeyer
1980 FxJj50: an early Pleistocene site in northern Kenya. World Archaeology 12:109-136.

Chavaillon, J., N. Chavaillon, F. Hours and M. Piperno
1979 From the Oldowan to the Middle Stone Age at Melka Kunture (Ethiopia): understanding cultural changes. Quaternaria 21:81-114.

Clark, J.D.
1970 The Prehistory of Africa. London: Thames and Hudson.

Gowlett, J.A.J., J.W.K. Harris, D. Walton and B.A. Wood
1981 Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. Nature 294:125-129.

Hewes, G.W.
1961 Food transport and the origin of hominid bipedalism. American Anthropologist 63:687-710.

Hill, A.P.
1975 Taphonomy of Contemporary and Late Cenezoic East African Vertebrates. Ph.D. Dissertation, University of London.

Isaac, G.Ll.
1969 Studies of early culture in East Africa. World Archaeology 1:1-28.

1976 The activities of early African hominids: a review of archaeological evidence from the time span two and a half to one million years ago. *In*: G.Ll. Isaac and E.R. McCown (eds.), Human Origins: Louis Leakey and the East African Evidence. Pp. 483-514. Menlo Park: W.A. Benjamin.

1978 The food sharing behavior of proto-human hominids. Scientific American 238:90-108.

1981 The earliest archaeological traces. *In:* D.L. Clark (ed.), The Cambridge History of Africa. Volume I. From the Earliest times to c. 500 B.C. Pp. 157-247. Cambridge: Cambridge University Press.

1981 Archaeological tests of alternative models of early hominid behaviour: excavation and experiments. Royal Society of London, Philosophical Transactions B 292:177-188.

1983 Bones in contention: competing explanations for the juxtaposition of early Pleistocene artifacts and faunal remains. *In*: C. Grigson and J. Clutton-Brock (eds.), Bones and Archaeology: Hunters and their Prey. Oxford: British Archaeological Record.

Jones, P.
1979 Effects of raw materials on biface manufacture. Science 204:835-6.

1981 Experimental implement manufacture and use: a case study from Olduvai Gorge. Royal Society of London, Philosophical Transactions B 292:189-195.

Keeley, L.H. and N. Toth
1981 Microwear polishes on early stone tools from Koobi Fora, Kenya. Nature 293:464-465.

Kroll, E. and G.Ll. Isaac
In press.
Configurations of artifacts and bones at early Pleistocene sites in East Africa. *In*: H.J. Hietala and P.A. Larson (eds.), Intrasite Spatial Analysis in Archaeology. Cambridge: Cambridge University Press.

Landau, M.L.
1981 The Anthropogenic: Paleoanthropological Writing as a Genre of Literature. Ph.D. Dissertation, Yale University, New Haven.

Leakey, M.D.
1971 Olduvai Gorge. Vol. 3. Cambridge: Cambridge University Press.

Lewin, R.
1981 Research News: Ethiopian stone tools are world's oldest. Science 211:806-807.

Lovejoy, C.O. 1981
The origin of man. Science 211:341-350.

Pilbeam, D.
1980 Major trends in human evolution. *In*: L.K. Königsson (ed.), Current Argument on Early Man. Pp. 261-285. Oxford: Pergamon Press.

Potts, R.B.
1982 Lower Pleistocene site formation and hominid activities at Olduvai Gorge, Tanzania. Ph.D. Dissertation, Department of Anthropology, Harvard University. Cambridge.

Potts, R.B. and P. Shipman
1981 Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. Nature 291:577-580.

Roche, H. and J.J. Tiercelin
1977 Decouverte d'une industrie lithique ancienne in situ dans la formation d'Hadar, Afar central, Ethiopie. Compte Rendus de la Academie de Sciences, Paris

Rose, M.
1976 Bipedal behavior of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. American Journal of Pysical Anthropology 44: 247-262.

Schick, K.
In preparation
Site formation processes considered as a guide to interpreting early sites in East Africa. Ph.D. Dissertation, Department of Anthropology, University of California, Berkeley.

Stiles, D.
1979 Recent archaeological findings at the Sterkfontein site. Nature 277:381-382.

Tanner, N.
1980 On Becoming Human. Cambridge: Cambridge University Press.

Tobias, P.V. and A.R. Hughes
1969 The new Witwatersrand University excavation at Sterkfontein. South African Archaeological Bulletin 24:158-169.

Toth, N.
1982 The stone technologies of early hominids at Koobi Fora, Kenya: an experimental approach. Ph.D. Dissertation, Department of Anthropology, University of California, Berkeley.

Washburn, S.L.
1960 Tools and human evolution. Scientific American 203:3-15.

Question Period V

Question: I wonder whether there is any direct evidence from these early hominid sites of the relative importance of gathering and hunting, and also as a sort of corollary, is there any direct evidence for sexual division of labour?

Isaac: The answer in brief is no. We don't have direct evidence for either. Plant foods normally don't have preservable residues. This is a problem up and down the archaeological record. We see the animal food much more clearly, and as Elaine Morgan hilariously points out, hunting has been grossly exaggerated in versions of prehistory, and with it the role attributed to males. We don't have direct evidence unless you take those plant tissue traces on the chert tool, as evidence of that. However, what I'm arguing is that basically, the food transport central-place system doesn't make very much adaptive sense without the emergence of some sort of balanced reciprocity between different members of society. To put it bluntly and crudely, the central location becomes a sort of market place where male and female members of a social group exchange commodities. So what I'm suggesting is some sort of an economic theory of the basis of human abilities. At some stage, certainly, plant food gathering was added, and I would suspect fairly early on, but we're going to have to struggle to find ways of demonstrating, and of measuring that.

Question: Do you have any ideas on how?

Isaac: How to find it? Find sites which preserve plant remains of some sort. Phytoliths may turn out to be a useful indicator. That's one that we intend to try.

Question: Have you done experimental work to explore the properties of vegetation of the kind that would have been growing around these early sites for things like bending and perhaps weaving a sleeping platform and nest in a tree in the way that gorillas and chimps do?

Isaac: We haven't done experimental work, of exactly that kind but two of our graduate students are now working on aspects of the structure of plant communities that grow in these kinds of places. They are starting mainly by looking at the potential food properties of these kinds of plant communities, but to be sure other kinds of characterizations also need to be investigated.

Question: In a book I read, I think called the *Innocent Killers*, exactly that picture comes out. The first scene is that these carnivores have a central lair. Next they have a division of labour. Those who did not have young went out and brought food back. Thirdly, they ate meat, and fourthly they had to carry the food back. In fact you have exactly the same pattern of behaviour with all animals that care for their young, e.g., birds, rodents, carnivores, and so on. One parent guards the young while the other collects food and brings it back for the family. There seems to be nothing remarkable about this behaviour in man.

Isaac: Yes, the closest parallel in mammals would be in the social carnivores. It's not a complete parallel. But it is the wild dogs and wolves that are particularly close. At times, when they leave the young in the den with "babysitters" and some of the adults remain to guard the den because wild dogs are fairly low on the pecking order of carnivores, and they're vulnerable. The rest of the pack will go out and, because they haven't developed carrying devices, they do it by what to us would be a rather distasteful way. They come back and they regurgitate food both for the young and the babysitter. This is a somewhat analogous system to the human pattern but it does not involve the radial movement pattern that in the human pattern covers a wider range of habitat types. In part it relates to the portability of the food, I mean I think that such a system is most likely to get under way if you have some highly portable food. And meat is that. Lovejoy has suggested that all this began before meat eating and that males who were taking the equivalent of chocolates to their girl friends were doing it in the form of berries and nuts. Well, you really can't carry enough berries and nuts to make a difference to the reproductive success of your girlfriend if you don't have some kind of tool; but a haunch of wildebeest may really provide useful food. So it's not that I want to play up meat too strongly, but it is highly portable food.

Question: Several years ago, artifacts were recovered from bed C at Omo which would be dated at about 2.5-2.75 mya.

Isaac: The position is, that we've had a succession of archaeological sites that were claimed to be dated 2.5 to 2.75 mya, and they've all crumbled down to 2 mya. At Koobi Fora some of the KBS sites we thought were 2.5 to 2.75 mya. Then, the assiduity of paleontologists, such as Basil Cooke, demonstrated that they were 1.9 mya, the same age as Bed I at Olduvai. The same fate befell member C artifacts, and they turned out to be probably in a fault block of G around 1.8-1.9 mya that had been mistakenly identifed as C. There are two localities, the gravel, which has some battered stones that may or may not be artifacts, but then as you go sideways from the gravel into floodplain silts, these have genuine artifacts. There isn't any doubt that these are genuine artifacts. The problem is that the geology of that part of the section hasn't been studied in detail. We know that at the top of the section you start to have cut-and-fill deposition. Layers were eroded and new layers laid in and then cut again. This occurrence of artifacts is above the highest dated horizon, only just above, but it is above. So until they're able to get back and do rigorous studies, I treat it as a possibility, but not as a confirmed instance, of artifacts at 2.5 mya. For the rest of East Africa, artifacts appear to come in with a big bang at 2 mya. In all sections younger than 2 mya they're quite common.

Question: Was the adaptive system that involved the transport of food and the feeding of young a new development at about 2 mya or does it go much further back, perhaps, as Lovejoy has suggested, before the adoption of bipedal locomotion?

Isaac: I don't think that I can choose between those two possibilities at the moment. What I can say is that we have archaeological evidence that some such system had come into being by 2 mya and we are only able to identify it because some hominids had started to create fossil behaviour in the form of stone tools. These identify the places that we are calling home bases. And it helps us identify the consumption of meat and so on, so without the stone tools we wouldn't recognize the system. I can't answer whether the system is older than the stone tools and created the demand for the stone tools, in part. It may well be somewhat older; your guess is as good as mine. What I would point out in relation to bipedality is that we have a great temptation, as modern humans looking back, to explain things in terms of their consequences...and most of the explanations of bipedalism have explained it in terms of the advantages which accrued after it had been adopted. But there is an interesting possiblity, and this is something that David Pilbeam is fond of pointing out, that bipedalism, like many other major shifts in evolution, was a preadaptation. That is, it may have arisen in a behavioural feeding context which later on became obsolete, and disappeared entirely. However, once bipedalism had happened it created other possibilities owing to the freeing of the hands, etc. I think we need to keep a very broad spectrum of interpretations for the origins of bipedalism and go after the evidence that will really allow us to distinguish them.

Question: For carrying, the handiest thing around would be animal skins.

Isaac: This is correct. Potential carrying devices are quite reasonably frequent on the African savanna. It may well be that, as Richard Lee said several years ago, that the basic human invention was the carrying device, making this way of life possible. And certainly in doing our fieldwork in Natron recently, we did pick up a piece of dried buffalo hide that, broken in half, would have formed two basin-like containers. We also broke off slabs of fig tree bark that made perfectly good trays. With a simple tray you could carry a small pile of berries. In fact that is how the Australian aborigines carry much of their gathered fruit. So it is a real possiblity. I entirely agree with Phillip Tobias that before the invention of stone tools there was a long period of the use of simple expediency objects like sticks and naturally sharp objects, and so forth; and that what we see with the invention of stone tools was the simple but dramatic discovery that you can break stone at will to generate sharp edges. It was probably not the beginning of tool use but just the use of making tools out of durable substances that we can still find.

Final Panel Discussion

Cooke: Well, Ladies and Gentlemen, this is the final section of the symposium, we now again have a panel discussion, I think we'll follow the same format that we did this morning and let the members of the panel start quizzing each other on matters particularly relevant to the last two talks, and then I have a substantial number of questions that we can get on with from the floor. Now has anyone of the panel have a problem for Glynn Isaac or Ralph Holloway?

Tobias: Can I raise one of the very last points that came up in Ralph's talk in the discussion time this morning? Why are there so few markings on the endocasts of hominids? I'd like to suggest one aspect which has occurred to me in my own study of endocranial casts. It's fairly obvious that the weight of the brain impinging on the side-walls of the skull throughout life, with the pulsation of the brain with every heartbeat, is going ultimately to imprint a pattern on the inner walls of the calvaria, or inner vault of the skull. Indeed it starts very young. Those impressions are at their best in juvenile and young adolescent individuals, and that is why our numerous adolescent fossils have better casts and give us better information than older ones. But, the question that always occurred to me, as Weidenreich pointed out about 1936 in his study of Peking man, is that the upper part of the endocranial cast is almost devoid of any markings, while the side-walls and the base are rich in markings. Now he didn't attempt to give any reason for that. He even identified a particular line where the well-marked area adjoined the poorly marked area. With his great love of inventing new names he called the junction line the "limen coronale." It occurred to me that perhaps gravity and the way in which one holds one's head may be the critical factors. After all, an animal holds its head in a particular position; and we hold our heads in a particular posture, for 90% of our lifetime. In that time, in an upright individual, gravity is going to lead the brain to impinge more heavily on the base and on the sides of the calvaria. We don't stand on our heads very much of the time. Therefore, in only relatively few of the total number of thousands of hours of a lifetime the brain is able, with gravity's help, to impinge on the *upper surface* of the vault. I can't help feeling that gravity is a very important factor. Indeed, if one looks at a four footed animal, whose head hangs down, the markings on the top of the cranium are just as good as the markings on the side and the base, which tends to give some confirmation to that view. Connolly I find had put forward the same suggestion independently in his study of endocasts. Some of the most informative areas that we'd like to get information from, including the telltale area of the lunate sulcus, just at the back of the top of the brain are poorly marked on hominid endocasts, probably for the same reason. Therefore the fact that the top of the endocast of australopithecus is smooth and featureless may provide a strange and unexpected confirmation of the fact that austrolopithecus walked upright. I believe that gravity perhaps has played a big part.

Holloway: (Post-discussion insert, Editor). While I would not rule out gravity as a factor relating to variation in the preservation of convolutional detail on the internal table of cranial bone, I believe the problem is far more complex, there being such great variability within species. Some 40 endocasts of *Pan paniscus*, (the pygmy chimp) have been made, about 38 for *Pan troglodytes*, the "common" chimp, and 40 for *Gorilla gorilla*, plus perhaps 20 to 30 each for *Hylobates* and *Symphalangus*. I have studied perhaps 150-200 for *Homo sapiens*. Almost all are adult, but a few juveniles have been processed also. Aside from one *P. troglodytes*, the lunate sulcus cannot be unambiguously observed on any of the endocasts. The O.H.12 hominid is an exception, and coming from Bed II of Olduvai, does show a nice pattern. There is one adult *Pan troglodytes* where, with a bit of guessing, almost every convolution appears on the dorsal surface. But then, most primates, including some prosimians, keep their heads fairly erect, and these animals, as well as new and old world monkeys, all tend to show what convolutions they possess on the dorsal surface of their endocasts. STS 60 from Sterkfontein, shows beautiful convolutional detail in the anterior portion, or the frontal lobe, quite a bit on the temporal, but none on the partial parietal lobe. Yet STS 5, "Ms. Ples", one of the ugliest specimens yet discovered as far as "endocast aesthetics" is involved, shows not a single gyrus or sulcus worthy of our labours. STS 19/38 is interesting too; the base shows detail, but not the dorsal portion. Taung is unique, of course, and a child; the next best endocast being the very distorted but convolutionally rich Hadar child AL-333-105, *A. afarensis*. Until the already exfoliating bone is taken off the Makapansgat MLD 37/38 posterior cranial specimen, we don't know anything except that MLD 1 shows no convolutional detail. The beautiful SK 1585 endocast from Swartkrans which Dr. Brain and Dr. Tobias allowed me to prepare many years ago, shows almost no dorsal cortical detail, but you can almost count the number of folia of the cerebellum! O.H.7 from Olduvai is a juvenile, and the partial parietal endocast shows not a trace of convolutional detail. All of the Lake Turkana material is terrible for detail, as erosion of the internal table of bone is common. I would simply conclude that the problem is multi-factorial; no single explanation suffices, whether gravity, age, sex, or species. Dean Falk (1980) recently made an interesting claim: the endocast for Taung formed prior to the dissolution of the dura mater. There is no empirical support for that claim either.

In all my comparative endocast work, there is only one chimp endocast in which every single gyrus and sulcus showed up.

Tobias: Was it a youngster?

Holloway: No, it was not, it was an adult. and an old one, and I can not explain for the life of me what this variability amounts to. And when I came down to South Africa, you know you have one of the most splendid endocast collections in the whole world, at the U. of Wits. I studied them this summer. The range of variability within the human groups of the faithfulness of the some of the gyri and sulci was quite remarkable. I think in the overall view, gravity has a great deal to do with it, but I think it must be a little more complicated than that.

Tobias: I wonder what is the mechanism of the removal of those impressions with aging? Perhaps it is the shrinking of the brain. We know that after the age of about 22 one's brain shrinks. Thereafter, as nerve-cells die off and are not replaced, progressively one's head gets filled with nothingness. Maybe then there is lack of a tight fit of the brain as the skull doesn't change. The lack of a tight fit and the lack of contact between brain and skull-vault may in fact remove the source of the pressure from the inner surface of the skull. But then what is the mechanism of smoothing the existing already-established markings? It's very odd.

Holloway: Processes of osteoblastic and osteoclastic moulding have not been thoroughly studied on cranial bone, particularly the internal layer. There are some old (age-wise) endocasts which do show some surprising detail, so the shrinkage theory is hard to accept without some empirical demonstration of variations in deposition and erosion of bone. After all, the outer layer of dura mater is periosteum for the internal table of cortical bone. The dura is very thick, and there is, in the underlying arachnoid membrane, a veritable cistern of cerebrospinal fluid particularly in the region of the Rolandic or central sulcus region. This makes the identification of that fissure just about impossible in the Hominoidea, and has led to the still-prevalent myth of our relatively large frontal lobe. Empirical anatomical data show nothing of the sort; we have about as much frontal lobe as expected for a primate of our brain size.

I always pass on this famous anecdote, which is prompted by Dr. Tobias' comments regarding shrinkage. By age 65, it is estimated that we have lost about 1/3 of our neurons in the cortex. The calculation I often make is that one Holloway lecture costs you about 350,000 neurons...but with some 10 billion to start with, you shouldn't worry unduly.

Cooke: I must say that's very discouraging.

Cooke: I did have a question from the floor that I might bring in at this point. It's what other clues from human ontogeny give us hints about human evolution?

Holloway: I have great trouble seeing brain embryological development as recapitulating phylogenetic changes, but then again, I am not adequately trained in neuroembryology. It certainly is an area to investigate very carefully, and I am partial to Stephen Gould's studies and suggestions regarding RNA controlling rates of development, and migrations of neurons at different times, work beautifully investigated by Rakic and his co-workers. I would imagine that if we compared very closely the neuroembryonic development of chimp and human, without access to rate and migration information, we would find precious little to differentiate between the two, except of course, the relative amounts of primary visual striate cortex, which is reduced in *Homo sapiens*. Needless to say, Broca's and Wernicke's areas (frontal and parieto-temporal lobes, respectively) would (or should be) prime targets for close attention. But I would most fervently hope and trust that chimpanzees would not be sacrificed just to suit our curiosity, and I doubt if there is enough embryonic brain material already collected for such an intensive investigation. We do tend to speak endlessly about brain size, and forget about the "wiring" of the brain and it is there that I believe more species-specific neuroembryonic events occur. These are hardly "trivia" as Jerison (1973) claimed, but rather one of the most important aspects of evolutionary change in different species' brains.

Cooke: Phillip, do you have anything to add on ontogeny?

Tobias: I fully agree with Ralph in drawing attention to Stephen Gould's work. It certainly seems that the brain during its individual development does go through some stages which recapitulate the probable phylogentic stages. One of the very interesting ones to which the late Prof. Lawrie Wells drew attention was the openness of the sylvian fissure or the lateral fissure between the temporal lobe and the base of the frontal and parietal lobes. In a young baby, that's wide open and one can look into the fissure and see the little island or insula of Reil without having to spread the lips. In certain living people, and in certain of the earlier fossil man endocasts one can see a poorly closed lateral fissure. There are suggestions, as the Dutch anatomist, Bolk, pointed out a number of years ago, of a number of recapitulative elements in the human brain and, of course, in the human skull. The other thing, Basil, that's so fascinating about the ontogeny is Brash's work at Edinburgh in which he showed that, although you might think that the skull is the tough hard entity that impinges on the brain and imprints the pattern on the brain, in fact it's the other way around. During the development of a baby and in a young child, the skull, as Brash put it, floats apart on a sea of expanding brain! It is the brain that calls the tune while the skull is the passive member.

Cooke: The human brain does funny things. But I think that the most appropriate question to turn to from those submitted is what evidence do we have for the beginnings of fire in the human record?

Wu: So far as China is concerned, regarding the use of fire, there we found ash, burned bones and wood at the site of Yuenmou. And also at Lantien. Of course there is much evidence in Choukoutien Cave so that use of fire by Peking Man seems to be definite. There is lots of evidence, many layers of ashes, burned bones, stones and many others. So the confirmed evidence of the use of fire by Peking Man is about 0.5 million years old. As to the other sites, the sites of Yuenmou and Lantien, some of our colleagues believe there is evidence of the use of fire, because Lantien is earlier than Peking man and Yuenmou is supposed to be dated at 1.9 mya, now maybe a little less than 1 million. But many of our colleagues believe the evidence is not definite.

Tobias: How does the age of the Choukoutien fire compare with the age of the hearth at Vértesszöllös in Hungary? That's also pretty old. I did once hear 350,000 for the Vértesszöllös site on the third terrace of the Danube, not far from Budapest.

Isaac: I think the only thing that can be said for the date of Vértesszöllös which is one of the oldest dated human habitation sites in Europe, is that it's younger than the latest geomagnetic reversal, so it's less than 700,000. And it's on up the faunal sequence a small way. Something in the neighbourhood of a third to half a million would be a reasonable guess, so that would be very much the same sort of age as Choukoutien. And to add to what Prof. Wu has said: there is an interesting pattern to the earliest occurrence of fire, namely, all of the oldest sites in the cold temperate zones, the zone with frozen winters, have fire in them. And this seems to make perfectly good sense, and it looks as if our ancestors had enough nous not to go into these regions until they had fire, but what it leaves undefined is how much older the control of fire was before the colonization of the cold zone. And what we've discovered in Africa is that the charcoal doesn't survive in these kinds of deposits; it doesn't even survive for a few tens of thousands of years mostly, unless you've got a protected situation like a cave. This means that the normal method of digging sites and looking for great chunks of black as evidence of fire doesn't work and it leaves us in ignorance of how old fire is in Africa. Some of you may have seen published in *Nature* late last year, a claim that there was fire represented at Chesowanja, a site dated at 1.4 mya. We also had one of our excavations at Koobi Fora dated at 1.5 mya that had some red patches in that I'm sure were burnt, because the physical tests imply so. However, the problem we face in East Africa is that we have in these beds abundant natural traces of bush fires. It's not difficult to find on the landscape traces of fire, and what we are going to have to learn is to distinguish controlled fire from wild fire. And that may be part of the problem that Prof. Wu is referring to at Yuenmou or Lantien. It's not enough just to find charcoal in a layer to prove that humans were making fire, because we know that natural fires occur as well. So it is a real challenge that faces archaeology.

Cooke: It's an interesting fact that in Africa there is a significant portion of the vegetation that produces seeds that do not germinate unless they are burned. So this means that natural fires are sufficiently widespread to be part of the inherent development of a whole biological system.

Other questions have come in which are appropriate at this time. This is a rather lengthy one. Glynn Isaac's food-sharing model is a very nice hypothesis; however, I'm not sure how it can actually be tested. I always thought that what makes a hypothesis scientific is its testability. How would one test this model? What evidence would be considered concrete evidence for food-sharing behaviour, what special distribution of stone and bone fragments would imply food-sharing rather than for instance a number of individuals or one, over a long period of time, gathering and consuming his or her own food? I like this model, it's logical but can it be proved in whatever sense an anthropological hypothesis can ever be proved?

Isaac: Basically it's often true in science that many comparatively large and sweeping hypotheses have to be broken into parts. For instance you can't deal with the "theory of evolution" as a whole. You can take a series of predictions out of it and see if they are met in the real world. I would argue that the food sharing model also has to be treated in a similar way. It has to be broken into parts — e.g. (1), is there evidence that food was repeatedly transported to one particular place? (We can show that it was). (2) Are the quantities of bones and artifacts such that it would seem reasonable to attribute them all to the activities of a single solitary hominid? (The answer would seem to be, no there are too many for that.) (3) If more than one hominid was involved at the same time, does it seem reasonable to suppose that each individual fed alone, not allowing the others any part of what had been carried to the place? (The answer to this is partly subjective, but observation of animal behaviour suggests one would not carry food to a social focus if other members of the group were to be precluded entirely from access).

So you see that by building up a series of propositions that can be judged, a case emerges. It is less than proof but it is a strong working hypothesis. As in all science, as soon as such a position is achieved it is the duty of researchers to try to knock down or revise the working hypothesis.

Holloway: There is another way of looking at these comments regarding food-sharing. The evidence *does* add to the probability that these were important behavioural advances. We know there exists a considerable degree of human offspring postnatal dependency, a period in which the young are immature, defenseless, and in need of protection by older social actors. There is evidence for meat-eating, albeit impossible to quantify. I find it very difficult to imagine the females of early *Homo*, or *Australopithecus* extracting meat for themselves while burdened with offspring unless there were clear patterns of sharing protein resources. It can't be empirically proven unless we get into a time machine and observe it, so one has to use it in a probabilistic sense. Most simply stated, without sharing in the past, and I really do believe it involved some kind of sexual dimorphism in division of labour, we wouldn't be here today to discuss the issues.

Cooke: Another interesting question has come up. Is there any way in which we can estimate population size at this kind of 2 myr old stretch of time? That is, let's say African population size.

Isaac: The answer in brief is no. But just a few observations that may be of interest to the asker of the question. Firstly, the artifacts in situations where stone is accessible are very common. So I would suspect that we're not dealing with very rare creatures. The other observation which may be of interest is that at Koobi Fora the skilled team of men who hunted for fossils went out and searched with equal intensity and skill for the bones of hominids and of any other primate and of carnivores. There were huge numbers of bones of ungulates, antelopes and wild horses and the like and pigs and so on, which they left alone, because they're in large quantities and only specialists in those groups collect them. But they collected hominids, primates, and carnivores with equal intensity. Of course it's a crude measure but the relative frequency they found each of these may be some sort of indication of relative abundance. And what turned out is that hominid bones of both species have the same sort of magnitude of frequency as the large carnivores, and the primates. The large grassland *Theropithecus* baboon is more abundant than the hominids, and the other primates put together. So put in these kinds of terms it looks as if the hominids may have had something like the abundance of the large carnivores in a modern game park and if you went driving around in a "Landrover" 2 mya ago you'd have quite a good chance, it would appear, of seeing one or two hominids, but there wouldn't be one behind every bush, if you see what I mean.

Tobias: Could I add to that? It's probably more likely that one would get an idea of what the group size might have been, rather than the total population. If we use models of living hunter-gatherer peoples, we find that those living in pretty extreme sorts of environments like the Kalahari desert, the !Kung or San people of the Kalahari desert, one finds that there are fairly wide tolerance limits on group size. There may be as many as a hundred and fifty but that's in the middle of the wet good season when food is abundant. Then when the dry season comes and the animals scatter in search of water, the San scatter and the group breaks up into smaller groups; there may be as few as two in a group, two young men who go off hunting together for the season and then reunite with the rest of the party in the following genial season once again. So the likelihood is, on that model, which pertains also to aboriginal societies, that during the hunting-gathering phase there were many groups, that each group was relatively limited in size. I would think that populations would have been dispersed as many nuclear groups, with varying rules governing interaction between one group and the next; whether you could marry or you could not marry into a neighbouring group say; or whether you had to marry into the neighbouring group and not your own group. These are the very conditions under which the so-called Sewall/Wright effect of genetic drift operates most vigorously. So there is a possible mechanism in that demographic structure of the population by which non-selective evolution and founder effects could have been quite important in certain areas under certain conditions.

Isaac: I'd like to add a note to that that may be of interest. It's hard to evaluate. Sites that we tend to think of as some kind of central place or homebase sites, from the very beginning of the Pleistocene until just before the emergence of agriculture, are very much the same size. If you get a well-preserved example of one that doesn't appear to be a multiple shifting episode thing, it is commonly of the order of 12 to 15, 16, 17 metres in diameter. The earliest sites have that size and the sites up until just before agriculture have that size and everything that looks like a decent site in between. Which may mean that human evolution, as Phillip has been suggesting, may have run most of its course with a modal size of group somewhere in the range of 15 to 30 individuals. This means that you have to think about the societies, the day to day face to face group, being quite small by our standards.

Cooke: It sounds as if the answer is that the individual group is of the order of an extended family rather than a tribe, that the overall density distribution is something like that of carnivores and that they form that sort of role in the food chain. It would be difficult to turn that into numbers unless we can get a census of the numbers of lions and leopards in Africa. Which I suppose we could do.

Question: What is the status of the taxon *Homo habilis*?

Tobias: I think it's a good species and I think it's the first species of the genus *Homo* to have appeared. I apologize publicly for my tardiness in publishing the formal account of the Olduvai *Homo habilis* type population, but I'm happy to tell you that I have finished the first 1000 pages of the manuscript which has gone to Cambridge University Press. If only they would spare me from the Deanship back home, I would be able to put the finishing touches to the last few bits and pieces that have to be completed. In that on the basis of about 150 different morphological markers, on the cranium, on the mandible, on the dentition, and to a lesser extent on the post-cranial bones, and on the endocranial casts (and we have a large number of *habilis* specimens from Olduvai), I believe the case for the species would be acceptable to most human biologists. Indeed, it has become increasingly accepted in published accounts in recent years. Ralph raised the point this morning, which ones am I calling *Homo habilis*? I certainly do regard Twiggy, Olduvai hominid 24, as a good specimen of *Homo habilis*, even though she was sat on by a passing elephant. I do consider Olduvai hominid 13, that's Cinderella, as a good *Homo habilis*, just a young damsel of 13 or 14 when she met her end. I think George, Olduvai hominid 16, is a good example; the "road-maker's mandible" as Mary Leakey called him. Olduvai hominid 37, is another, and there are some 12 to 15 individuals in greater and lesser degrees of incompleteness from Olduvai alone. To those have to be added large numbers of isolated *habilis* teeth from Omo, *habilis* specimens from East Turkana, such as KNMER 1470 and KNMER 1813 and specimens now also from South Africa, from member 5 in the Sterkfontein formation and possibly from member 1 in the Swartkrans formation. So we have quite a fair population of *Homo habilis*, the ranges, the statistics, all bespeak something different from *A. africanus*, different not only in time, (it's more recent) but different in morphology, as testified largely by markers at the head end of the body. We do have finger bones and metacarpals, and they are different from those of *Australopithecus*. I have a student doing a Ph.D on those at the moment. We have a clutch (perhaps a phalanx - Ed.) of finger-bones; I showed you a few of them here on the screen yesterday. All in all, I think the status of *habilis* will be seen to be very highly confirmed when this work comes out. Again I beat my breast and apologize that it has been in incubation for such a long time.

Cooke: I think you overlooked the possibility that Twiggy was sent through the Canadian parcel mail service.

Tobias: It's better you said that than I did!

Cooke: You have I think pretty well answered another question that came in...How are you defining *Homo*? On morphological grounds or on the initial appearance of stone tools? I think the answer is very clearly on morphology not on the appearance of tools. We regard the appearance of tools as hopefully coincidental.

Isaac: That's very important.

Tobias: And supportive.

Cooke: There is a question here for Dr. Wu. Could you give us some idea of what are the procedures for reconstructing such badly distorted skulls as that found in Lufeng?

Wu: We have tried to reconstruct the crushed skull of *Ramapithecus* because as I showed on slides in both views from the top and the base, it is almost complete, but the trouble is how can I push it up from flat pieces? So I have tried but not yet successfully. I am not yet finished. Every part of the skull like the orbits, each part of the skull I have tried to push it back up and make a complete skull. We have tried a tentative reconstruction. But it was not very satisfactory and so I didn't show it on the slides. We're still going to do more work. But Dr. Pilbeam last year visited our institute and he suggested we might use the computer to make the reconstruction but I don't know how to...Maybe we should ask Alan Walker how to make a reconstruction with a computer but we haven't tried it yet.

Cooke: Alan Walker has used computer techniques for matching bone fragments and been quite successful. As far as I remember, when Twiggy was being decrushed, the technique was to literally pull it all apart keeping reference to where the bones were, and put it together again taking due account of the curvature and the natural relationships between bones. So it was literally taken down to the small fragments and reassembled. I hope that answers the question.

Tobias: That took Ron Clarke the best part of 3 years. Unflattening Twiggy. I may just mention the kind of problem: if there's anyone here in need of intelligent occupational therapy, George, that very lamentable creature from Olduvai (he's called Olduvai George) was found just after a herd of Masai cattle had found him. And there's evidence to believe that he was an absolutely complete skull including the mandible and all the teeth, all 32 adult permanent teeth, when the herd of Masai cattle walked over him before the Leakey family got to him and carried him on their dung-encrusted hoofs for about 150 yards down the cattle trail to the water. About 900 or 950 pieces of George were picked up. Of the cranium, the calvaria or vault, has been reconstructed from a mere 128 pieces; that was about 2 years' work. And there are about another 700-800 pieces in sundry small matchboxes, cigarette boxes, chocolate boxes, cigar boxes, waiting to be reassembled. Some of them are smaller than one's fingernail, tiny fragments with newly broken edges. Someday that total skull will be re-assembled. However, from 128 pieces we got a very nice impression of the curvature and the structure of the vault. The individual pieces were not crushed and therefore they still have their anatomical fine detail.

Cooke: Any jigsaw puzzle enthusiasts will be welcome as volunteers. Another question, rather off our general track but interesting. Do you anticipate any new applications of new technological techniques, such as nuclear magnetic resonance, which might be used in order to locate valuable fossils at a dig?

Isaac: The answer is I wish that I knew that we could find things underground by some kind of remote sensing. I suppose there is a theoretical possibility, given that there is a small mechanical difference between bone particles and sharp stone tools, relative to the matrix in which they are encased but I don't know of any plans to develop it or anyone who is holding out the money that it would obviously cost to develop such instrumentation. So the answer is that I don't know of any such prospects around the corner.

Cooke: I think on the other hand, the developments in the last few decades have been tremendous, and they've been largely through the application of new and unexpected techniques, for example the paleomagnetic time scale, thermoluminesence dating, amino acid dating and uranium-thorium series dating. All of these tools were really not even thought of 20 years ago and they are very important parts of today's research. I think the answer is that undoubtably there are going to be new techniques. One of the most exciting, for example, is the development in Canada of new techniques for doing radiocarbon dating, from extremely small samples by using essentially the technique of the mass spectrometer. So it will be possible to take a pinhead or smaller sized piece of carbon and get an accurate date. This is going to open up a totally new perspective.

Isaac: Can I just mention another really promising new body of techniques, the recognition that different dietary patterns leave an imprint in the composition of bone? For instance, the ratio of ^{13}C to normal carbon is affected by the plants or the position in the food chain of the organism feeding. And similarly strontium and calcium ratios are affected by the position of the organism in the food chain. The methods are still in the pioneering phase, but we may get information that we badly need. For instance, the question came up earlier about the plant-animal ratio in early hominid diets. If some of those techniques can be made to work in that time range, we may have information that reflects an average diet, not just the refuse from one or two meals.

Cooke: There are also some quite exciting investigations being made with electron microscopy on tooth enamel, to see what the patterns of micro-scratching are. Provided you eliminate the problems of the preparator and also the calipers of those who come and measure these specimens, it's possible to get a great deal of information about the diet and the way in which the teeth were used. It's also been discovered in these electron micrograph studies that one of the worst enemies of teeth is dental toothpaste. So I don't know what you do, change to gel I suppose!

Tobias: Floss! Basil, if we're going to mention actual new techniques in the study of fossils, perhaps one should just draw attention to a landmark publication, the particular new Canadian publication on the X-ray study of fossils. Although it's just 75 years since the first fossil was studied by an x-ray, just a couple of years after Röntgen got his Nobel prize for discovering x-rays, this is the first systematic attempt to subject the teeth and jaws of a large percentage of the world's available fossil skulls to x-ray studies. It is quite a landmark in its own way. I don't think I should let the moment pass without paying tribute to Mark Skinner and Geoffrey Sperber who have been responsible for this work. (Skinner, M.F. and Sperber, G.H. *Atlas of Radiographs of Early Man. New York: Alan R. Liss, Inc. 1982*). But I wanted to add to what Prof. Cooke said. The scanning electron microscope is proving valuable in all sorts of ways, such as studies that may throw light not merely on surface structure like the enamel prisms, but also on the pattern of abrasion, erosion or attrition of the surface of a particular part of the body. And talking of that, one can get inside the pelvis, the innominate bone, by means of x-rays. One of my research students (I. Suzman) has found new evidence for the uprightness of the Australopithecines in the arrangement of the leashes of trabeculae inside the bone. An animal that walks upright like ourselves, has the trabeculae oriented in such a way that they go right down to the weight-bearing point where the head of the femur sits. In four-footed animals with a quadrupedal locomotion, in apes for instance, one finds a totally different pattern of the internal arrangement of the trabeculae and it's only the x-rays that have yielded us this new information.

Cooke: Prof. Tobias is obviously the one most under attack and there's a letter here from a sceptic who says "Have you examined *A. afarensis* material yourself or are your statements based on written descriptions"? And he resented the fact that in my summary this morning, I showed only one of Dr. Tobias' slides and only one set of measurements as an exemplification of this rather great similarity, whereas Dr. Tobias I think had a large number of slides indicating a large number of similar characters. But I think that Dr. Tobias should spring to his own defense.

Tobias: As far as the originals are concerned I have seen a good percentage of them but by no means all. And I have not made a close personal study of the fossils. My remarks if you'll remember were based upon the statements made in the diagnosis of the new species. In a recent publication, (*American Journal of Physical Anthropology*, April, 1982) there are a number of tables in which point by point was picked up from the stated diagnostic features of the supposed new species, *afarensis* and it was shown that those statements did not pass muster when the same criteria were applied to the Transvaal *A. africanus* fossils. I confined my statements to the species diagnosis as published by the authors of the species, White, Johanson and Coppens. I do have a very full set of casts, which have been generously made available to me, of a large number of the Hadar fossils and some of the Laetoli. I've seen a number of the original Laetoli fossils as well.

Cooke: Thank you, another question. I'm not sure if the answer is yes or no. Would someone care to comment on the hypothesis put forward by Owen

Lovejoy that bipedalism developed in response to a certain reproductive strategy. I think Glynn Isaac's prepared to stick his neck out.

Isaac: Well, basically I suppose I like it because it makes a very good precursor for the model I was trying to sell you this afternoon. That is to say Lovejoy's suggested male first provisioning could have been a step in the direction of the behaviour I was calling food-sharing. These terms are not quite synonyms, provisioning refers simply to the transport of food by an adult breeding pair to feed its young, whereas food-sharing in human societies at least in recent times is a broader distribution of foodstuffs. Basically, Lovejoy's suggestion is that bipedalism is an adaptation for carrying and that the advantage, the importance, of carrying was that the males were improving their reproductive success by helping their females to acquire food to feed themselves and to support lactation and feed the young. Since the males had to carry food, they needed their hands free to do that, and so they needed to be bipedal. Lovejoy is suggesting that male provisioning goes right back to 4 million years ago and was the first shift in the direction of hominids. Socio-reproduction is a system that's very little discussed in most accounts of human evolution. Lovejoy argues that provisioning was followed by bipedalism, followed by the expansion of the brain. Lovejoy makes it in his exposition, in my view unnecessarily difficult, to accept the hypothesis by first of all ruling out tools, saying they couldn't have had any part in it, and second of all, by ruling out meat, although without a container you can't carry enough vegetable foods around to feed your mate usefully. So Lovejoy has had to relent on that. In a later part of the paper he says that they would have had to use simple carrying devices. This exclusion of meat is unnecessary. We don't know whether meat was part of diet at this stage but he rules it out in advance even though meat is the most portable of all foodstuffs.

Cooke: So you don't think that a handful of nuts is comparable to a tray of caviar and champagne!

Tobias: Can I build on one other aspect of Lovejoy's theory? When one is quadrupedal, and one stands in this position, there is a warm sheltered concavity underneath here which contains the very sensitive ventral skin of the body, the relatively hairless skin which is much more sensitive than this rough, hairy, dorsal skin behind. The creature also has breasts inside the concealed area and the posture protects the genitals. When you come upright like this, see what the consequences are: there is a full frontal exposure of the breasts, genitals and the ventral sensitive skin, in a kind of face-to-face situation between one biped, one tottering biped and another. I can't help feeling that he's on to a very important aspect there. It's not quite the aspect that Glynn stressed, but one which I have picked up and believe it is something terribly important in the psycho-sexual development of our kind of bipedal hominid with our curious, all-year-around sexual receptivity and loss of the oestrus, and other aspects which govern the sex life of man.

Isaac: Just let me clarify. I think he made the details of his hypothesis unnecessarily difficult but I think the suggestion that the first shift may have been in the socio-reproductive system is a very interesting one. The problem now is how do you set the hypothesis up so as to test it?

Holloway: Tobias' sudden shift of posture from a quadruped to a biped is simply too much fun to let go of here: a fine opportunity to put together love, need for foreplay, and carrying, if not food, then perhaps bouquets of flowers, all rolled into one locomotor adaption. But in seriousness, sexual dimorphism in secondary sexual characteristics (permanent breasts, hair and fat deposition *and* distribution, e.g., in the pubic region) should not be ignored, although without time machines, there is not a single reasonable hypothesis to test, based on current living primates. I have tried again and again to make this point in the literature, because I regard endocrine-target tissue interactions as something that did change during the evolutionary transition from an ape-like Miocene precursor to early hominids. There was simply too much at stake regarding increased infant and child dependency, and social nurturance, and "something" had to change in the complemental structure of relationships between females and males. Unfortunately, we are speaking of soft-tissue anatomy, physiological and cognitive behaviour, none of which fossilizes. This is one reason why the sexual dimorphism of the modern *Homo* corpus collosum is interesting. It is not so much a matter of "biological fatalism" that interests me here, but rather that the difference, and it does appear by prenatal week 26, is a possible clue to "heritage". It is very premature, however, to make too much out of this at the present time, without a much fuller knowledge of the variability of the dimorphism in larger samples, and its existence or lack in our closest living pongid cousins, the chimpanzee and gorilla. This is a different area, given the sexual sociopolitical atmosphere that we live in today, but I do have a strong feeling that there was a complemental pattern of behaviour.

Cooke: So *Australopithecus* was the first flasher!

Tobias: That'll make headlines, Basil. Take care!

Cooke: Another question, on a different track. Does acceptance of the shorter molecular control dating scale imply that in the last 5 myrs, the gorilla and the chimpanzee have had to change their locomotory pattern twice; from quadrupedalism to brachiation and from brachiation to quadrupedal locomotion. Does the panel see this as a problem and if so to whom? I think to the bipedal hominid. I think this is perhaps beyond the panel! On a more specific note, again I think directed to someone who's acquainted with the Berkeley material. They ask for our opinion on Tim White's analysis of cut marks on the *Homo* skull from Ethiopia. He states in his article in *Science* in September, 1982 there are cutmarks under the eye and under the cheekbone. He wonders if they were defleshing the skull. Also is there any more evidence for cut marks on other skulls dating to this time period of around 300,000 BP? I don't know the Bodo skull.

Isaac: Just before the skull went back to Ethiopia Tim White showed me these cut marks, and I can briefly comment on and amplify the published report. The first thing to get straight is the Bodo skull is a very impressive skull in the sort of way that Prof. Jacob's skulls from Java are. It is massive, it is close to the world's record for hominid skull thickness which makes it pretty thick. It has great brow ridges and it is clear that this in life would have been a very impressive alpha male. It is at the transition of *Homo erectus* to *Homo sapiens*, but probably most people would put it into *Homo sapiens*. Beyond that, there *are* cut marks and they are in exactly the same location as the cut marks on medical school skulls where the flesh has been taken off to prepare the skull. They are on the zygomatics, just above the maxilla, across the scalp and on the occipital. They are also inside the orbits showing that they took the eye tissue out, using sharp edged tools. So it is absolutely clear that the meat was taken off this skull. The evidence is what you could go to a court of law and testify on but the question then arises - WHY? It is intriguing for us to speculate but there is nothing in the specimen that will give one the answer. One could argue that it was cannibalism, but it could just as easily be that this really was an impressive individual that they really wanted to have to carry around, this impressive relic of the individual, and they took the flesh off the skull to keep it as a relic. And that would be just as good an explanation. What seems certain is that the cut-marks represent behaviour after death that was emotionally and ritually charged.

Tobias: Basil, arising out of that, I wonder if I could reopen with Teuku Jacob the question of cannibalism. He gave us 3 reasons why he rejected the idea of routine cannibalism. Now it seemed to me, thinking about cannibalism as a regular source of nutritional supplementation, whether it could serve as a major factor in the diet. I don't know if there are any examples in the world. Perhaps somebody could tell me of any peoples known in the recent historic period who were nutritional cannibals. But cannibalism, where it exists at present and in the recent past, always has a ritual aspect to it rather than a nutritional aspect; you don't eat that man's testicles or heart or brain because you can't get any other source of first class protein; you eat it because you want particular qualities of that person in your own body. And I wonder whether, Teuku, you wouldn't care to comment on those broken bases of skulls of *Homo erectus*—and don't forget that wherever we find *Homo erectus* in Europe, in Africa, in Asia, in 95% of all the skulls we've got, the base has been broken. When you come up to Neandertal man, there are neater breaks on the base and they have clearly been deliberately broken. One can see symmetrical butterfly-shaped incision marks around the foramen magnum, say in Monte Circeo and Saccopastore in Italy and elsewhere. Quite clearly, that was deliberate ritual and skull after skull is collected in a cave with the bases of the skull broken open at the part where the base of the skull is thinnest, where you can get into the brain most easily. You'll find this continuing into the Bronze Age. It continues into the historical period and in the 19th century, Pacific islands missionaries reported the practice still in existence, where it was tied to a very elaborate ritual of naming a newborn son. According to Alberto Blanc, there were only a limited number of names to go round. If a new son was born to a family, then somebody had to give his name to that new son. But you couldn't have 2 people called by the same name and so the older person bearing the name had to be sacrificed. This was not murder; it was a ritual method of christening the new little baby. The head was removed off the holder of the name, the base of the skull was very neatly opened, the brain was extracted, cooked with sago, eaten by the father of the newborn son and then that newborn son could bear the name of his namesake, and incidentally, his namesake's skull was kept on his mantelshelf, so to speak, until it became that little chap's turn to pass his name on to someone else. Now, I'm not suggesting that it was as elaborate a ritual a couple of hundred thousand years ago, in Peking Man or in Java Man, or in Olduvai or in Mauritanian *Homo erectus*, but it does seem remarkable that we have a continuity of breaking the bases of the skull over a ½ million years or more, leading to historically very refined, highly complex rituals. Is it not possible, Teuku, that the skull breaks that one sees, almost without exception (there are only a couple of exceptions, that you have found yourself), testify to a possible ritual cannibalism in this long historical sequence which is indisputable from Neandertal onwards, but in its earlier rough-and-ready manifestations is disputable, as distinct from nutritional cannibalism?

Jacob: I have two very large skull collections with broken bases. One collection is from the Bronze-Iron Age of Bali, dating about 2000 years ago; many skulls have broken bases, and actually when you have seen some of the exavations on the beach of Gilimanuk in West Bali, when you lift up the skulls then the sands inside the skulls just break the skull base. So you get this in a few cases, and they are really the same thing as in Ngandong skulls. And if you take photographs of the skulls from Gilimanuk, with proper lighting, you can get the same skull bones as Ngandong as published on many occasions. Then the other skull collection is from 18th century Batavia. The skulls were recovered in 1972 during urban reconstruction in a church yard called the Portuguese Church of the 18th century. The dating was by means of smoking pipes. The recovered pipes are dated according to a pipe collection in a tobacco musuem in Groningen. So in the newspapers of that time people were thinking about the Chinese mass murder in 1740 which is notorious in Indonesia, in Dutch East Indies history. But what we saw during the study of the skulls are just breaks made by latter-day cannibals. In the excavation during this interruption of urban reconstruction, it's not according to the rules of the art. But if you take photographs of this skull collection of the church yard of Jakarta you get the same impressions as the Ngandong skulls. But these skulls are all Caucasoid and the reason why the skulls are in the Portuguese church is because the mass on Sundays is in Portuguese. So in these two collections of skulls with broken bases, without any evidence of human hands, I don't think that you should call this cannibalism, just by surgical fractures seen on the skull base. For nutritional purposes you can take up the example in Harrison Salisbury's book on the Leningrad siege; I think that is for nutrition, and also the plane crash in the Andes. I think that is also for nutrition; but you don't call these people cannibals, although they do eat for protein. So I think because of these two large samples of skulls without bases, and you can see the irregular structure of the fractures, I don't think from this evidence cannibalism should be concluded.

Tobias: The only thing that worries me is why none of our curiously thin-skulled *Australopithecus* or *Homo habilis*, even the robust Australopiths, display nothing like *Homo erectus* fractures. Not one of them has a broken base. In almost every one of them we have a perfectly preserved foramen magnum and the whole basal structure, whether it's from cave sites in South Africa or from open sites, even with some secondary redeposition perhaps in East Africa. In all of these earlier skulls, we don't see this fracture pattern. It's always foxed me why the thin-skulled ones, which you might have thought were weaker and more liable to breakage, lack basal breaks, but from *erectus* onwards you've got this sort of lineage of broken bases.

Jacob: It's not the thinness which is evenly distributed. It's the uneven thickness and the numerous fissures and foramena and so on that give different pressures on the skull base. So if you have the calvarial bones with even thickness you don't have problems whether they are thick or thin. But in the *erectus* skulls from Java, the occipital bone around the foramen magnum is just as thin as in modern man, 1.5 to 2 mm. By comparison, on the squama it's about 7 to 10 mm thick. So this uneven pressure on the skull bones with many fissures and holes on the base of course causes breakage. You can see this in *Homo sapiens* as I mentioned earlier. So I think that as tools should be evidence of human hands, the structural breaks in this case should be our guideline for concluding natural fractures and not representing cannibalistic behaviour.

Cooke: The next question is whether at Olduvai there is only *Homo habilis* and the robust Australopithecine or is there some material that doesn't appear to be either?

Tobias: There is no material at Olduvai that I am convinced is morphologically *Australopithecus africanus*. Member I and Member II contain only *habilis* and *A. boisei*. From the upper part of II upwards we have *erectus*, the Olduvai hominid 9 and so on, and right at the very top is *Homo sapiens*.

Cooke: Any other questions?

Question: This is directed towards Drs. Jacob and Wu as well. The *Homo* has been found in both your areas. Do you think the early predecessors of *Homo* in your countries walked in from Africa or evolved *in situ* or in your region? Or is it multi- evolution in different parts of the world?.

Cooke: I'm afraid I'm not really clear on the question but I gather it's directed to Dr. Jacob and you're asking whether he regards *Homo erectus* as an immigrant or a local development?

Jacob: Well I don't know. As you see the useful theory is that the islands are on the periphery of the area of human evolution, so everything which is there now or has been there in the past should come from other places. But I think the more logical position to take is that any area at any one time in history could be in one aspect or another, a centre of evolution. A centre means that man developed there. But as we see at the moment that many fossils have been found in Africa, continually through a long time range. But, we also have other evidences from for example Asia, which is a very large continent and has not been thoroughly explored yet. So other places besides Africa should be kept in mind that could also be a good place for evolution. For the moment I don't argue for any one place as the cradle of mankind, whether they are immigrants or transmigrants or locally developed. And this is actually not very important at this stage of our theory of human evolution. It's nice to think that one place of origin could be recognized. So I cannot answer your question whether they are immigrants or not.

Cooke: Perhaps we could direct the question to Dr. Wu, whether he feels there is any evidence for a mainland Asian origin for man.

Wu: I don't think so. (I agree with Dr. Jacob).

Cooke: He says " I don't think so," but I'm sure he'd very much like to find something in Lufeng or higher up that might change his mind. Certainly it's startling, the new information that's coming out of Asia.

Jacob: Dr. Cooke, by Asia I think we should include Europe because geographically Europe is just a part of Asia.

Cooke: Or maybe the other way around. Are there any other questions?

Tobias: Could I just say a word about Africa?

Cooke: By all means.

Tobias: It is a point to bear in mind that Africa is just under one quarter of the world's habitable land surface. It's about 24% or something of that kind, and it is the largest land-mass that straddles the Equator. Into it you can fit all of Europe, China and India! Large parts of Africa, most of it, is equatorial, tropical and sub-tropical, essentially warm regions. Man, the applied physiologists tell us, is a warm-adapted creature. Perhaps this argues in favour of an African origin of man. Of course, once his cultural plasticity evolved, he could move into a far greater range of habitats. Armed with fire, cave-dwelling and perhaps rude clothing, he could move even into colder regions. This culture was an added dimension that opened wider horizons to him. I can only suggest that, when you consider all the chunks of world available, *a priori*, Africa would seem to be the most suitable site of the origin of man from the point of view of its size, its climate, and its disposition vis-a-vis the Equator and the Tropics.

Cooke: Thank you, there was a question from the back?

Question: Yes, my question is very similar to the answer already given. It concerns the same sort of subject matter. It seems to me that there was some support from this panel for the Coon-Weidenreich model of human evolution over the last ½ million years, rather than the alternative or opposing model that's been supported by William Howells for example over the last 40 years. I wondered if members of the panel would comment on that.

Tobias: What is referred to here is a theory known as polyphyletism, the idea, put forward by Carleton Coon, building on the earlier ideas of Weidenreich, built on the yet earlier notion of Klaatsch in the last century, that man evolved into *Homo sapiens* in several different centres from pre-*Homo sapiens*, presumably from *Homo erectus*. Carleton Coon actually suggested five different living races of *Homo sapiens*, major races, each of which had its *erectus* predecessor, and that there was an *erectus/sapiens* threshold, so that man in Africa went from *erectus* of Africa to *sapiens* of Africa, and man of Europe went from *erectus* of Europe to *sapiens* of Europe etc. This is the basis of that idea known as the polyphyletic theory of the origin of man. When it was first put forward we knew very little about genetics and population genetics. I don't think anyone today takes that theory at all seriously, the idea of there being an *erectus/sapiens* threshold, at which different groups in different parts of the world, (subject to the same mutations which we've got to postulate), would cross over, ending up belonging to the same species, interfertile on a world scale. I don't think there is any strong support for that idea today at all. I don't know that there's ever been any. Carl Coon's book on "The Origin of Races of Man" never gained much support and was severely criticized in fact. It flies in the face of all that we know of human population genetics. But what might happen, and this is where Dr. Wu's suggestion of yesterday is very interesting, is that, although man has become a branching and anastomosing reticulate population, perhaps for the last 1.5 myr, in some areas, certain mutations might have had a very ancient history, like the shovel-shaped incisors in China. The people in that area might still to this day have a higher frequency of shovel-shaped incisors, the Mongoloid peoples, than other peoples. Nevertheless, that gene is found also in Africa and in Europe and in Australia etc. In other words the boundaries are not the rigid boundaries that Carleton Coon demanded.

Question: My interpretation of Carleton Coon, after just reading his book actually, was that he did believe that inter-subspecies peripheral gene flow did occur, but that there was not enough of it to wipe out the basic racial traits. That's my reading of his book, anyway. Other than that, I agree completely with what you said. What about the Howells' model, which basically postulates that you do have these different centres of origin, I think mainly for *Homo sapiens*. What he was mainly concerned with, I don't think he said exactly where, but it was somewhere in the Near East and then spread out from there and sort of eliminated all the other varieties from the previous radiation of *Homo erectus*. Do you support that idea?

Tobias: Only to a very limited extent. But I think it is tenable within narrow limits and over narrow periods of time. But let's hear what Glynn wants to say.

Isaac: Well it's been an issue of debate for fifty or sixty years and I don't think any final solution is yet in sight. In some regions, for instance Western Europe, you can still make quite a good case that the Neandertals were replaced, that is, there was a movement of new genes, new people coming in. In other regions the change over looks more like a gradual transition. In this connection molecular evidence is contributing. Working with mitochondrial DNA which is only transmitted in the ovum so that it only goes down the female line so you don't have to deal with the problem of crossing over in fertilization, it turns out that the diversity of mitochondrial DNA would not allow you to have a bottleneck, that is, a very small population that is ancestral to all living humans, inside the last ½ myr. That would knock out the most extreme form of what you're calling the Howells' hypothesis.

Tobias: It is interesting that there could well have been a very ancient dichotomy between some of the major races or constellations of people and others. We've had that reference from Prof. Wu, and I mentioned the interesting early appearance of one trend of dental reduction in Africa, and another trend in Asia. It's interesting that all the molecular biological evidence puts Europe and Africa very close together. If one made a cladogram, one would show Europe and Africa had come from a common ancestor much more recently than the Eurafrican stock had separated from the Mongoloids. There is a much earlier break between the two latter groups, and it may well be that geographical isolation came into being for quite a long time. Not enough to produce speciation, but enough for swirlings of genes on either side of the divide to develop and become high in frequency, like shovel-shaped incisors and other factors of that kind. That doesn't go as far as Carleton Coon does. I certainly don't accept the full flush of his theory.

Cooke: I think we are bordering on the topic for another symposium, on the races of man. I also think that our time is running out. I was asked to try and summarize the highlights of this meeting and I find it impossible. It's been very diverse. We've enjoyed the expertise of the leading exponent from China, Prof. Wu, the leading exponent from Java, Prof. Jacob, Prof. Tobias who is one of the leading members of the group that worked in Africa, Dr. Holloway who has a universal acquaintance with the brains of man and his predecessors, and Glynn Isaac who is one of the principal protagonists of detailed study of sites from the tool point of view. So you have been exposed, whether you realize it or not, to a great deal of very new thinking and very new material. And to me, this is the important part of the congress. I think that the bringing together of this group has been exciting, I hope you've all enjoyed it. For my part and on behalf of the other panelists I would like to express our gratitude to the University for inviting us, for having its 75th anniversary and for including us in this occasion, to the Chancellor and the President, and all the members of the staff of the University who have done so much to make this a success. Above all, I think we all owe a deep debt to Dr. Sperber who is sitting quietly in the corner pretending not to exist, whose brain-child this was and I think that he deserves the warmest congratulation on the success of this conference. I think it has been a success and I will ask him to come and close the meeting. Dr. Sperber.

Sperber: Dr. Cooke, symposiasts, ladies and gentlemen, thank you very much for you very kind remarks. Your continued presence here at this late hour indicates the high level of interest that this symposium has engendered. And I for one have enjoyed enormously the interaction between geologists, anatomists, paleoanthropologists, brain-specialists, and behaviourists. This has been one of the most exciting symposia I believe has taken place on this campus. I wish to thank the symposiasts for having contributed to this enormous level of interest that most of the audience have expressed to me. We have ranged over several million years of human prehistory during the course of the symposium and I believe that this symposium has in turn contributed significantly to the history of the University of Alberta in the celebration of its 75th anniversary and that it will become a landmark of our celebrations. The publication of the proceedings of this symposium in the *Canadian Journal of Anthropology* will provide a permanent record of this fascinating conference that will form part of the archival history of the University of Alberta.

I further propose to dedicate the ensuing publication to my mentor in the field of human evolution, Raymond Arthur Dart, Professor Emeritus of Anatomy at the University of the Witwatersrand, who first described the genus *Australopithecus*, and who is celebrating his 90th birthday on 4 February 1983. The publication of these proceedings accordingly will commemorate two anniversary celebrations — of an institution and of a man who has become an institution.

I would call upon you at this time to record your appreciation to the symposiasts in the customary manner of primates... Thank you very much. This brings the proceedings to a close.

Atlas of Radiographs of Early Man

Mark F. Skinner and Geoffrey H. Sperber

Atlas of Radiographs of Early Man is the first book of its kind that provides researchers and scholars *in the dental* and paleoanthropological fields of research with information about the unique—and at one time unavailable—raw data on hominid morphology. This **Atlas** is the most comprehensive collection of radiographs of fossil hominids ever assembled and includes a number of specimens never illustrated before.

Atlas of Radiographs of Early Man is a remarkable source of information illustrating and describing in detail the anatomy of teeth and jaws of early man. For each specimen, the Atlas provides the following information: the geographic origin of the specimen; the geological, archaeological, and chronological context of the specimen; a taxonomic designation, an anatomical summary of the parts preserved, and a detailed description of the structures illustrated in the radiograph; dental age; comment; and radiographic view. A total of 463 illustrations ranging from early hominids (dating back 2 to 3 million years) of Sub-Saharan Africa to later specimens from the last 50,000 years of European prehistory are included. A total of 48 sites are represented, including some from North America.

The **Atlas** also examines ontogenetic and phylogenetic irregularities in the internal anatomy of teeth and jaws of prehistoric man. Of particular significance are the illustrations of dental maturation in the jaws of the Neanderthal man, some of which date back to Europe's last ice age. There is an extensive series of radiographs of South African hominid cheek teeth showing interesting, and sometimes bewildering, differences in the size and shape of the pulp chambers.

Atlas of Radiographs of Early Man is an invaluable research tool for the serious student and professional in the fields of paleoanthropology, paleodemography, hominid dental evolution, archaeology, anthropology, and vertebrate paleontology.

CONTENTS

List of Radiographs
Foreword
Acknowledgements

Part I Introduction
Purpose and Scope of the Atlas
Format of the Atlas

Part II Radiographs

Sub-Saharan Africa
Ethiopia • Hadar • *Tanzania* • Olduvai • *South Africa* • Makapansgat • Sterkfontein • Taung • Kromdraai • Swartkrans • *Zambia* • Kabwe (Broken Hill)

North Africa
Algeria • Ternifine • *Libya* • Haua Fteah

Europe
Gibralter • Devil's Tower • Forbes's Quarry • *France* • Bruniquel Lafaye • Bruniquel les Forges • Cap Blanc • Châteauneuf-sur-Charente • Farincourt • Fontéchevade • Isturits • Lachaud • Laugerie-Basse • La Madeleine • Mas d'Azil • Le Morin • La Pique • Le Placard • La Quina • Roc de Cave • Roc de Sers • Rochereil • Les Roches • Rouset • Saint Germain La Rivière • Solutré • *Belgium* • Engis • *British Isles* • Badger Hole • Mother Grundy's Parlour • *Spain* • Parpalló • *Italy* • Archi Hill • *Austria* • Miesslingtal • *Germany* • Ranis • Weimar-Ehringsdorf • *Czechoslovakia* • Mladec • *Yugoslavia* • Krapina

Miscellaneous Areas
Israel • Mugharet-es-Skhul • *Indonesia* • Trinil • *Canada* • Old Crow

Literature Cited

Index of Specimens

In Europe, the United Kingdom, and the countries of East and West Africa order from your bookseller or from: ***John Wiley & Sons Limited • Baffins Lane • Chichester • Sussex P019 1UD • England***

Atlas of Radiographs of Early Man
Mark F. Skinner and Geoffrey H. Sperber
LC 82-13989 ISBN 0-8451-0218-4
Size: 7" x 10" 350 pages
U.S. $70.00 postpaid if prepaid

Alan R. Liss, Inc.
150 Fifth Ave.
New York, N.Y. 10011