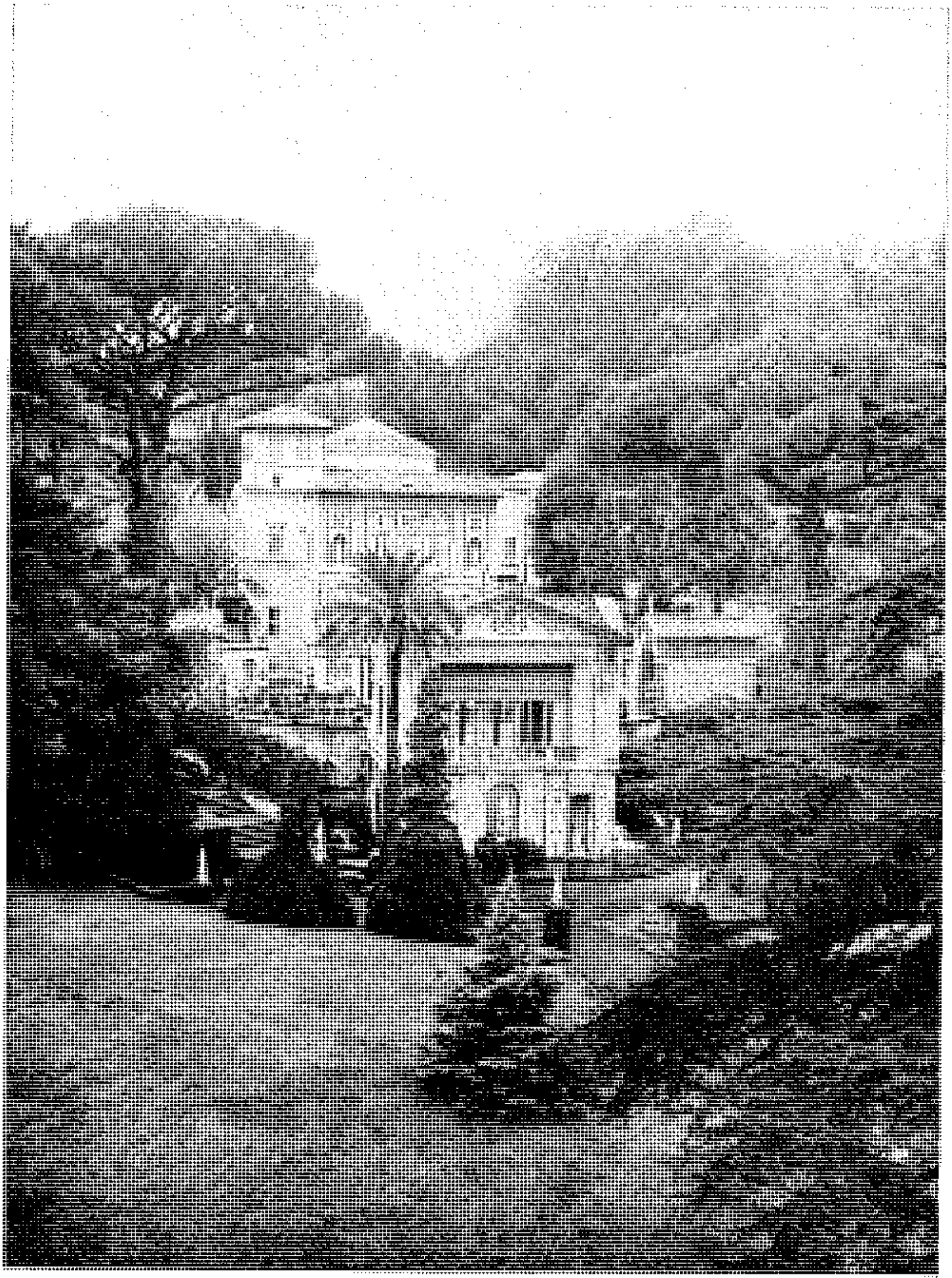


PONTIFICIAE ACADEMIAE SCIENTIARVM SCRIPTA VARIA

50

WORKING GROUP

ON:

RECENT ADVANCES IN THE EVOLUTION OF PRIMATES

May 24 - 27, 1982

EDITED BY

CARLOS CHAGAS

PONTIFICIA
ACADEMIA
SCIENTIARVM

EX AEDIBVS ACADEMICIS IN CIVITATE VATICANA

MCMLXXXIII

INDEX

SCIENTIFIC PAPERS

FOREWORD

From the 24th through the 27th of May 1982 a group of scientists met at the Casina Pio IV in the Vatican to discuss the recent advances in the knowledge of the evolution of primates. This meeting was organised by the Pontifical Academy of Sciences. The interest in organising another meeting on the subject came from the desire to conciliate data obtained from different approaches. The data originating from anthropopaleontological observations placed the ape hominid lineages split as long as 20 million years ago. This early divergence hypothesis is based on the fossil record of the Ramapithecus, dated from 7-16 million years, admitted as a hominid. The other sources of information come from Cytogenetics, Molecular Biology and Biochemistry,, in which comparison is made of results of determinations obtained from man, apes and monkeys. To these lines of research one should add paleontoimmunology, a rather recent field of work.

The late divergence hypothesis infers from the various data thus reached that the split occurred about 5-7 million years ago. The Ramapithecus may thus be placed in the hominoid category, a proposition which can be accepted by the anthropopaleontologists. It seemed reasonable to the participants to accept that in this event the data obtained by molecular biology and biochemistry are not inconsistent with the known fossil record. The chromosomal data presented indicate that man and chimpanzee are closer entities than man and other primates. They suggest also that species differences are more closely related to the position of genes in the chromosomes than to the genetic composition of the chromosomes.

The Working Group agreed that many aspects of the problems under study are still unsolved. These are, as examples, the precise time of the branchings or the role of environment in the appearance of bipedalims. There was quite a general consensus that the theory of divergent descent to man and other primates is supported by a mass of evidence but that *there is cause for differences of opinion in various matters, such as species formation and the mechanisms of evolutionary change.*

I have no intention of summarizing the discussions held. The objective of this introduction is only to express my admiration for the spirit of collaboration of the participants and their willingness to contribute, without any bias, to the progress of knowledge. This spirit pervaded the long but cheerful hours of the meeting.' I am very thankful to all of those who came to the Vatican leaving their working surroundings and interrupting for a week their productive life to contribute to the aims of the Pontifical Academy of Sciences. With their brilliancy and devotion to their scientific interest, they have turned our working sessions into one of the finest and most exciting meetings at which I have ever been present. The wealth of information presented in this booklet is a proof of their value and good will. However, each paper and the summary express the opinion of their authors.

I wish to express especially my sincere gratitude to Prof. Yves Coppens, without whom I would not have been able to convene the meeting, and to Prof. Perlman who prepared the summary. This summary is included as an annex to the papers presented. I would like also to extend my thanks for the continuous help they are giving to me, to Father Enrico di Rovasenda, Director of the Chancellery of the Pontifical Academy of Sciences, to Mrs. Michelle Porcelli-Studer, to Mrs. Gilda Massa and to Mr. Silvio Devoto. Without their aid the work of the Academy could not be pursued.

February 1983

CARLOS CHAGAS
President of the
Pontifical Academy of Sciences

LIST OF PARTICIPANTS

Prof. E. Boné, S.J., Université Catholique de Louvain, Laboratoire de Paléontologie des Vertébrés et de Paléontologie Humaine, Bâtiment Mercator, Place Louis Pasteur, 3, B-1348 Louvain-la-Neuve, Belgium.

Prof. Y. Coppens, Musée de l'Homme, Palais de Chaillot, 75117 Paris, France.

Prof. R. Doolittle, Department of Chemistry, University of California, La Jolla, California 92093 USA.

Prof. B. Dutrillaux, Université de Paris, Faculté de Médecine, Institut de Progénèse, 15 rue Ecole de Médecine, Paris VIe, France.

Prof. L.O. Greenfield, Department of Anthropology, Temple University, Philadelphia, Pa. 19122, USA.

Prof. J. Lejeune, Université de Paris, Faculté de Médecine, Institut de Progénèse, 15 rue Ecole de Médecine, Paris VIe, France.

Prof. J.M. Lowenstein, School of Medicine, University of California, San Francisco, Calif. 94143 USA.

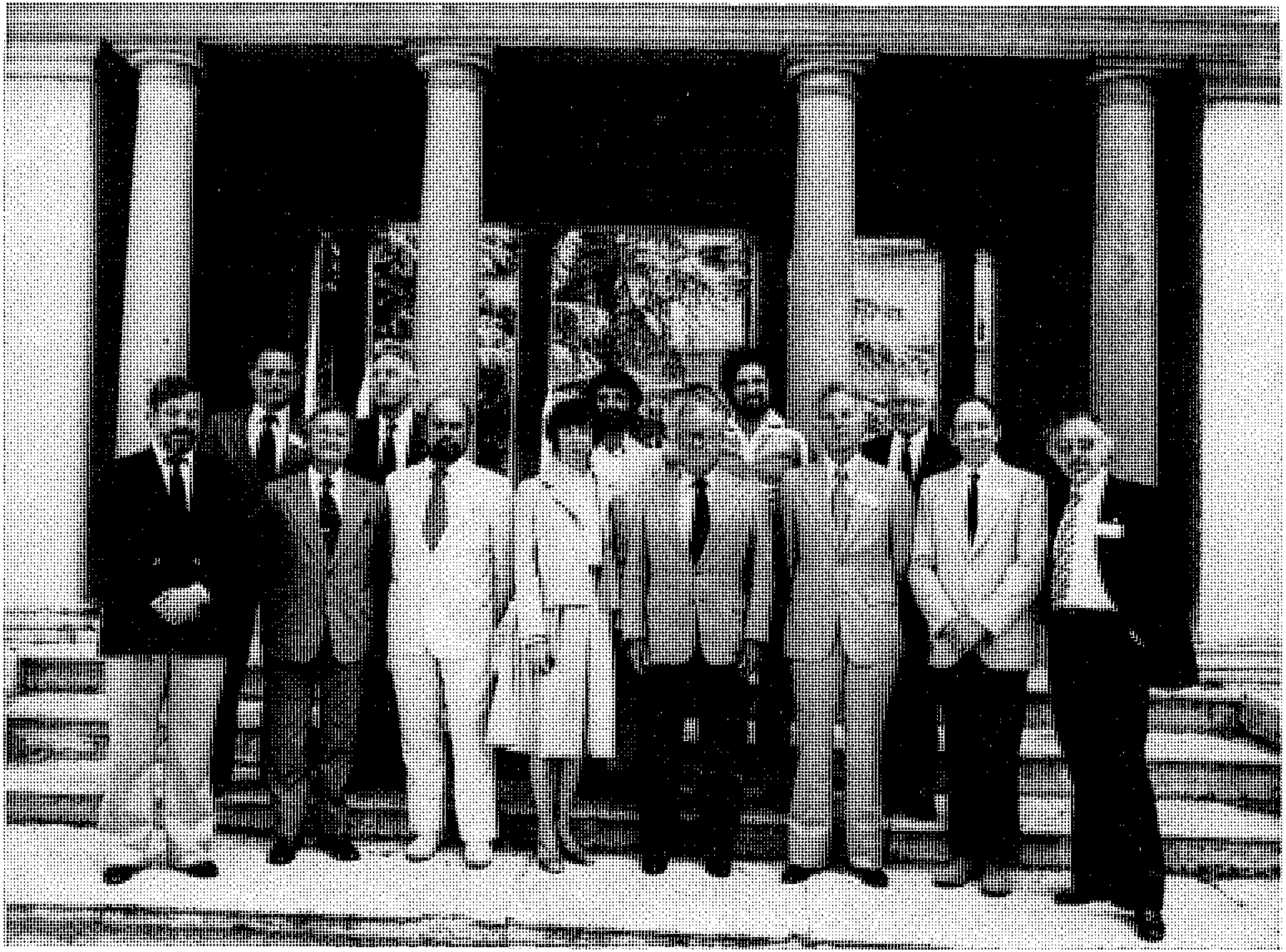
Prof. C. Pavan, Instituto de Biologia, Universidade Estadual de Campinas, 13100 Campinas, São Paulo, Brazil.

Prof. D. Pilbeam, Department of Anthropology, Peabody Museum, Harvard University, Cambridge, Mass. 02138 USA.

Prof. G. Sermonti, Via Felice Giordano 15, 00197 Roma, Italy. 808517(

Prof. E.L. Simons, Director, Duke University Center for the Study of Primate Biology and History, 3765 Erwin Road, Durham, North Carolina 27705, USA.

Prof. P.V. Tobias, University of the Witwatersrand Medical School, Hospital Street, Johannesburg 2001, South Africa.



SCIENTIFIC PAPERS

LES PLUS ANCIENS FOSSILES D'HOMINIDES

YVES COPPENS
Professeur au Muséum national d'Histoire naturelle de Paris

Face à certaines déclarations de biochimistes et de cytogénéticiens suggérant une séparation Paninés-Hominidés très récente (4 à 5.000.000 d'années), la principale question que doit se poser le paléontologiste est de savoir quels sont les restes les plus anciens connus dont il dispose et qui soient attribuables à coup sûr à des Hominidés (au sens restreint du terme (¹)).

Si l'on exclut la dent isolée découverte à Lukéino dans le bassin du lac Baringo au Kenya et datée de 6.500.000 ans et le fragment de mandibule encore porteur de sa première molaire recueilli à Lothagam, sur la rive sud ouest du lac Turkana au Kenya et datée de 5.500.000 ans, la réponse à cette question est la suivante: les plus anciens restes d'Hominidés certains dont dispose le paléontologiste sont tous est-africains: ce sont ceux de Laetoli, en Tanzanie, de Kanapoi et de Chemeron au Kenya, d'Hadar et de Bodo en Ethiopie; ils dépassent 3.500.000 ans et atteignent, pour certains, les 4.000.000 d'années.

Qui sont donc ces Hominidés de 3.500.000 à 4.000.000 d'années?

Groupés d'abord sous le nom d'*Australopithecus afarensis* (Johanson, White et Coppens, 1978), ils sont, à notre avis (Coppens, 1981 a et b, et 1982) de deux sortes, l'une très archaïque et l'autre étonnamment moderne.

La forme la plus archaïque des deux est celle de loin la plus représentée. On peut la caractériser par:

(¹) Nous n'employons Hominidés qu'à partir de la dichotomie Grands Singes africains - Hommes; il s'agit donc d'une famille qui ne recouvre que deux sous familles, celle des Australopithécinés et celle des Hominidés. Rappelons que la position extrême opposée, employée par F.S. Szalay et E. Delson (1979), place sous le concept d'Hominidae, les Hylobatinae, les Ponginae et les Homininae.

— une petite taille;
— un crâne de très petite capacité;
— un fort prognathisme alvéolaire;
— un palais long et très peu profond;
— une arcade dentaire longue, étroite, aux bords rectilignes;
— des apophyses zygomatiques très développées;
— des apophyses mastoïdes grandes et aplaties;
— des cavités glénoïdes larges mais peu profondes;
— une face large et massive;
— une mandibule de petite taille, avec arcade dentaire subrectangulaire;
— une région incisive relativement étroite;
— des incisives centrales supérieures grandes;
— des incisives latérales supérieures réduites;
— ces dents centrales et latérales pourvues d'un fort tubercule basal du côté lingual;
— des canines supérieures relativement grandes;
— une P^3 supérieure à moitié vestibulaire plus longue que la moitié linguale;
— une P^4 supérieure à moitié linguale plus longue que la moitié vestibulaire;
— une P_3 inférieure à parfois une seule cuspide vestibulaire;
— des diastèmes entre la seconde incisive et la canine supérieure;
— entre la canine et la P_3 inférieure (Johanson, White et Coppens, 1978);
— un membre supérieur archaïque, en partie comparable à celui d'*Australopithecus*, avec, à l'humérus, un sulcus intertubercularis (gouttière bicipitale) profond et étroit;
— une insertion du muscle supraspinatus plutôt longue;
— l'indication de muscles abducteurs du bras, coapteurs de l'épaule et fléchisseurs de l'avant-bras sur le bras bien développés;
— un aplatissement de l'epicondylus lateralis, situé plus haut que le capitulum humeri;
— une position centrale de la fossa olecrani;
— une margo lateralis soulignée par une crête assez forte;

— mais aussi une double trochlée;

— à l'ulna une tuberositas ulnae longue et étroite;

— une incisura trochlearis longue et étroite et sur le radius, une tuberositas radii et un collum radii longs et étroits (Senut, 1981) un membre inférieur archaïque, différent de celui d'*Australopithecus*, avec, au fémur, les 3 caractères traditionnels de l'Homme, liés mécaniquement entre eux de manière évidente;

— l'obliquité de la diaphyse fémorale;

— la saillie de la lèvre externe de la trochlée fémorale et le profil elliptique du condyle externe;

— mais, en plus, une épiphyse distale s'inscrivant schématiquement dans un rectangle fortement asymétrique par rapport au plan parasagittal passant par le milieu de la trochlée;

— avec nette prépondérance du côté interne sur le côté externe;

— une échancrure intercondylienne plus large que haute un peu comme chez le chimpanzé, avec légère inflexion du bord interne en forme d'arc de cercle;

— et au tibia une exceptionnelle proximité des épines tibiales entre elles et une convexité du plateau tibial externe, en contraste avec la concavité du plateau tibial interne (Tardieu, 1979);

— un bassin à l'ilion en pression, raccourci;

— une région sacrée renforcée, un sacrum élargi incliné vers l'arrière;

— une aile iliaque développée latéralement et un ischion court, incliné vers l'arrière (Berge, 1980 et Berge et Ponge, sous presse).

La forme la plus moderne des deux est celle, de loin, la moins représentée mais elle l'est tout de même par suffisamment d'éléments différents du squelette pour être parfaitement prise en considération.

Elle se caractérise, en particulier, par un membre supérieur moderne, semblable à celui d'*Homo sapiens* avec, à l'humérus, une faible saillie de l'epicondylus lateralis (épicondyle), un faible développement du capitulum humeri, en vue distale et pas de crête latérale à la fossa olecrani:

— au radius, une tuberositas radii et un collum radii trapus (Senut, 1981);

— un membre inférieur moderne, semblable à celui d'*Homo sapiens* avec, au fémur, outre les 3 caractères traditionnels déjà énoncés, obliquité de la diaphyse fémorale;

— saillie de la lèvre externe de la trochlée fémorale et profil elliptique du condyle externe;

— une épiphyse distale s'inscrivant schématiquement dans un carré, symétrique par rapport au plan parasagittal passant par le milieu de la trochlée, et une échancrure intercondylienne plus haute que large;

— au tibia, des épines tibiales avec, entre elles, un écartement important, tel que le massif épineux s'encastre très précisément dans l'échancrure intercondylienne, ce qui est caractéristique du genou humain, et une concavité des plateaux tibiaux, la concavité du plateau tibial externe étant un peu plus légère que celle du plateau tibial interne comme dans le genou humain (Tardieu, 1979).

Si maintenant on examine la diagnose d'*Australopithecus* révisée par Phillip Tobias en 1967, on constate qu'il n'est pas simple d'y faire entrer la forme la plus archaïque décrite précédemment. *Australopithecus* est en effet défini comme un genre d'Hominidae que distinguent les caractères suivants:

— capacité endocrânienne relativement petite, allant d'environ 360 à 640 cm^3, avec une moyenne d'environ 500 cm^3;

— crâne fait d'ossements relativement minces, rendus robustes, par endroits, par de fortes superstructures ectocrâniennes et par une pneumatisation remarquable;

— bourrelets susorbitaires fortement construits;

— orbites de modérées à nettement hautes avec une hauteur moyenne plus basse que chez les Pongidés;

— tendance, chez les individus à fortes dents jugales, à la formation d'une crête sagittale basse dans la région fronto-pariétale du calvarium;

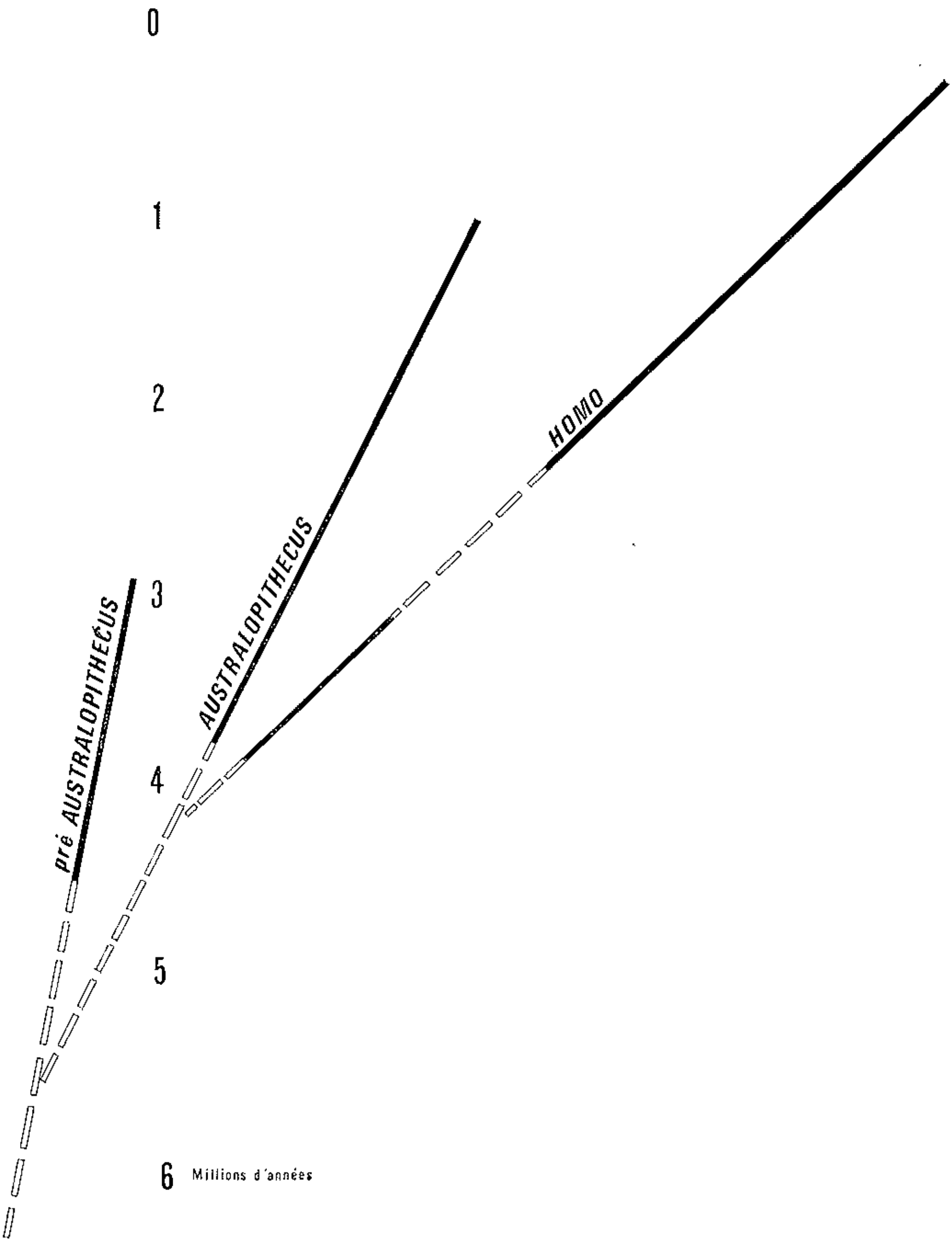
— condyles occipitaux bien en arrière du milieu de la longueur antéro postérieure du crâne, mais dans le même plan coronal que les orifices auditifs externes;

— foramen magnum bien en avant, sur la base du crâne;

— plan nuchal de l'occipital s'élevant à seulement une courte distance au-dessus du plan de Francfort et regardant généralement beaucoup plus vers le bas que vers l'arrière;

— inion bas et généralement proche du plan de Francfort;

— crête nuchale basse, pas en continuité avec la crête sagittale chez les formes à forte denture;



Proposition d'arbre phylétique des Hominidés.

— torus occipital léger dans les formes à denture modérée;

— développement de l'apophyse mastoïde pyramidale de modèle hominidé typique dans sa morphologie et ses rapports anatomiques, cavité glénoïde large médio-latéralement et de peu de profondeur, mais construite sur le modèle Hominidé (notamment dans les inclinaisons et la courbe de sa paroi antérieure et l'inclinaison vers le haut du plan prégénoïde avec une apophyse entoglénoïde prononcée et, quelquefois, un certain développement d'une apophyse post-glénoïde);

— porion élevé au-dessus de la ligne nasion opisthion;

— mâchoires robustes et massives, variation individuelle importante, menton absent ou légèrement indiqué;

— surface symphysaire relativement droite ou en retrait;

— contour de l'arc mandibulaire interne en V ou en U ouvert;

— arcade dentaire parabolique sans diastèmes;

— canines spatulées, de taille modérée, s'usant à plat à partir du sommet;

— prémolaires et molaires relativement grandes, notamment dans le sens vestibulo-lingual;

— première prémolaire inférieure bicuspide avec cuspides subégales, molarisation prononcée de la première molaire de lait inférieure, augmentation progressive de la taille des molaires inférieures permanentes, de la première à la 3ème;

— M^3 supérieure souvent plus petite que M^2;

— squelette des membres conforme, dans ses principaux traits, au type Hominidé mais différent d'*Homo* par le prolongement vers l'avant de la région de l'épine iliaque antérieure supérieure;

— la petite taille relative de la surface sacro iliaque;

— la position relativement basse de la tubérosité ischiale et le prolongement vers l'avant de l'échancrure intercondylienne du fémur.

Lorsque l'on compare la description de la forme la plus archaïque des niveaux de 3.500.000 à 4.000.000 d'années à cette diagnose, pourtant la plus « généreuse » parmi les diagnoses successives du genre *Australopithecus*, on se rend compte qu'il faudrait élargir considérablement cette dernière pour y faire entrer la forme ancienne. Il conviendrait, par exemple, d'ajouter « avec parfois des diastèmes » à « arcade dentaire parabolique sans diastèmes »; ajouter « parfois de grande taille » à « canines spatulées, de taille modérée »; ajouter « parfois unicuspides » à « première prémolaire inférieure bicuspide à cuspides subégales »; il faudrait aussi compléter par « épiphyse distale du fémur pouvant s'inscrire dans un rectangle fortement asymétrique par rapport au plan parasagittal passant par le milieu de la trochlée », « échancrure intercondylienne du fémur parfois plus large que haute », « exceptionnelle proximité des épines tibiales entre elles chez certains individus et convexité du plateau tibial externe chez ces mêmes individus », « double trochlée possible de l'humérus » etc...

En autres termes, il paraîtrait plus normal de traiter la forme la plus archaïque des deux Hominidés de 3.500.000 à 4.000.000 d'années comme un genre différent et pourtant suffisamment proche du genre *Australopithecus* pour qu'ils se rangent tous les deux dans la même sous famille des Australopithecinés.

Comme la forme la plus moderne est présente dès 4.000.000 d'années (Kanapoi) aux côtés de la forme la plus archaïque (Bodo), comme ces deux dernières et la forme qui leur est intermédiaire (*Australopithecus*) sont toutes trois beaucoup trop voisines pour ne pas être apparentées, comme la forme la plus archaïque a un membre supérieur proche de celui de la forme intermédiaire et différent de celui de la forme moderne, comme la forme intermédiaire a un membre postérieur proche de celui de la forme moderne et différent de celui de la forme la plus archaïque, je ne vois pas d'autres moyens de les associer phylogénétiquement que le suivant: un premier rameau représenterait la forme la plus archaïque que l'on pourrait provisoirement appeler Pré-*Australopithecus*; ce rameau strictement est-africain prendrait naissance très profondément, peut-être à 6.500.000 (la dent de Lukéino lui appartiendrait) ou 7.000.000 d'années et vivrait une existence autonome jusque vers 2.700.000 ans (âge des derniers restes fossiles qui lui soient attribuables et qui proviennent des gisements de l'Omo), époque à laquelle il s'éteindrait; mais ce rameau aurait donné naissance dès 5. à 6.000.000 d'années à un second rameau, celui des *Australopithecus*. Ce second rameau vivrait lui-même une existence autonome (passant d'ailleurs par des rameaux plus petits, représentant ses espèces successives, disposés comme les plus grands), s'étendrait à l'Afrique méridionale et s'éteindrait vers le million d'années. Mais ce second rameau aurait donné naissance, dès 4. à 5.000.000 d'années, à un troisième rameau, celui de l'Homme. Ce dernier rameau, étonnamment continu contrairement au précédent, passerait par trois grands successifs en même temps qu'il conquerrait le monde.

Pour répondre donc aux déclarations des biochimistes et des cytogénéticiens, le paléontologiste est en mesure de dire que dès 4.000.000

d'années il se trouve en présence de plusieurs Hominidés, dont certains si modernes qu'ils peuvent être assimilés, en tout cas provisoirement, au genre *Homo*. Cette contemporanéité qui est aussi une sympatrie, le conduit à proposer une filiation en inflorescence, filiation qui l'oblige à « plonger » jusqu'aux environs de 7.000.000 d'années au minimum pour envisager la séparation d'avec les grands Singes africains.

Et avant? Il n'est pas impossible, aux environs de 7.000.000 d'années, que la population de Primates, ancêtres communs des grands singes africains et des Hommes se soit trouvée divisée par l'effondrement de la Rift Valley. Cet accident tectonique qui a entraîné un partage des précipitations, abondantes à l'ouest, réduites à l'est, a, du même coup, soumis les deux moitiés de la population en question à des régimes de plus en plus contrastés: très humide, entraînant une continuité du paysage couvert à l'ouest, beaucoup moins arrosé, entraînant une ouverture du paysage à l'est. Gorille et Chimpanzés représenteraient les formes adaptées à ces savanes boisées et à ces forêts de l'ouest, Australopithèques et Hommes, les formes astreintes à la vie au sol et à la vigilance dans les prairies et les savanes claires de l'est.

REFERENCES

BERGE C., *Biométrie du bassin des Primates, application aux primates fossiles de Madagascar et aux anciens Hominidés.* Thèse de doctorat de 3ème cycle, Paris 1980, t. 1, pp. 160, t. 2, pp. 71.

BERGE C. et PONGE J.F., *Les caractéristiques du bassin des Australopithèques* (A. robustus, A. africanus *et* A. afarensis) *sont-elles liées à une bipédie de type humain.* In: Ives Coppens, Les Australopithèques. « Bull. et Mém. de la Soc. d'Anthrop. de Paris », sous presse.

COPPENS Y., *L'origine du genre* Homo. *Les processus de l'hominisation, l'évolution humaine, les faits, les modalités.* Colloque international du C.N.R.S., Paris 1981, pp. 55-60.

COPPENS Y., *Le cerveau des hommes fossiles.* C.R.A.S., exposés sur le cerveau, t. 292, supplément à la vie académique, Paris 1981, pp. 3-24.

COPPENS Y., *Les origines de l'homme, histoire et archéologie.* Les dossiers. « Le premier Homme », *60*, Paris 1982, pp. 8-15.

JOHANSON D., WHITE T. et COPPENS Y., *A new species of the genus* Australopithecus (Primates: Hominidae) *from the Pliocene of Eastern Africa.* « Kirtlandia », *28*, Cleveland 1978, pp. 1-14.

SENUT B., *L'humérus et ses articulations chez les Hominidés plio-pléistocènes.* « Cahiers de Paléontologie (Paléoanthropologie) », Paris 1981, p. 141.

SZALAY F.S. et DELSON E., *Evolutionary History of the Primates.* New York 1979, p: 580.

TARDIEU C., *Analyse morpho-fonctionnelle de l'articulation du genou chez les Primates. Application aux Hominidés.* Thèse de doctorat de 3ème cycle, Paris 1979, t. 1, p. 117, t. 2, p. 26.

RECENT ADVANCES IN KNOWLEDGE OF THE EARLIEST OF THE EGYPTIAN OLIGOCENE (INCLUDING THE MOST ANCIENT KNOWN PRESUMED ANCESTORS OF MAN)

ELWYN L. SIMONS
Director, Primate Center and Professor of Anthropology and Anatomy Duke University
Durham, USA

The generic names *Aegyptopithecus* and *Propliopithecus* have been coined to refer to the two oldest known types of apes, or "ape-like" catarrhines, both of which are recovered together from deposits of the same age in the Oligocene badlands of Egypt. Although the nonhuman Higher Primates, both catarrhine monkeys and apes, occur today in Asia as well as Africa, it seems that the first ancestors of the Old World Higher Primate group, suborder Anthropoidea, arose in Africa from unknown migrants that reached the Dark Continent in the Eocene Epoch, most probably having come from Europe. The two genera *Aegyptopithecus* and *Propliopithecus* are usually placed in the family Propliopithecidae while species of two other smaller, more monkey-like genera *Parapithecus* and *Apidium* are placed in the family Parapithecidae. The seven species of these four genera described to date all come from the middle or upper levels of the Fayum Oligocene stratigraphic section, north of north Africa's largest lake, Birket Qarum, in hadland exposures lying about 70 to 80 kilometers southwest of Cairo, Egypt. Besides these seven early catarrhines, two other species have been found in the lower Oligocene deposits of the Fayum. These are *Oligopithecus savagei* and a new species to be named "*Qatrania*", Simons and Kay (in press, 1982). These two forms come from the same quarry (Quarry E) and together they represent the oldest known undoubted members of man's mammalian suborder: Anthropoidea.

The introduction of the human, catarrhine monkey and ape common ancestor into Africa might have been as early as 50 million years ago. Just as Africa was for long a mystery to explorers it yet remains a mystery to understanding the early part of the age of mammals. Practically nothing is known of African land mammals during the first thirty million years of the Cenozoic Era or "Age of Mammals". Only a few continental, or nearshore, sediments that might contain mammal (and primate) fossils seem to have been deposited anywhere in Africa during the Paleocene and Eocene Epochs, when many land mammals have been found in France, particularly in Normandy, the Paris Basin and near Quercy in South-Central France. In all these parts of France, Paleocene and Eocene age primates occur abundantly. It is generally supposed that creatures related to these European primates may have found their way southward from Europe or Asia into Africa and there under unknown circumstances gave rise to the ancestors of apes, men and monkeys.

First documentation of Primates related to monkeys, apes and men anywhere in the Old World, thus, comes from the Fayum badlands about 80 kilometers southwest of Cairo, Egypt. There, some thirty-five million years ago ancient rivers were building out a delta into the ancestral Mediterranean Sea. Log-jams spread out on the delta in great profusion, and, at the site of one such deposit (Quarry E) two tiny jaws of primitive higher primates, *Oligopithecus* and "*Qatrania*" have been found buried near the fossilized logs. These two "dawn" anthropoids are compared in figure 1. These fossils, the oldest Fayum primates, appear to represent connecting links between the somewhat younger ape and monkey-like forms occurring there, *Aegyptopithecus*, *Propliopithecus*, *Parapithecus*, and *Apidium*, and certain Eocene tarsierlike prosimians, the omomyids. Since both species are known essentially from but one fragmentary half-mandible their exact position in the family tree of higher primates remains uncertain. Even so, *Oligopithecus*, named in Simons, 1962, had by 35 million years ago already lost all but two premolars on each side of each jaw. It had a honing wear-surface on the front one of each premolar pair and this tooth, thus, sharpened the back side of the upper canine. Such an interlocking canine-premolar mechanism is typical of Old World Higher Primates or Anthropoidea. In consequence, it seems that *Oligopithecus* had already reached the Higher Primate stage of development and could not be sensibly ranked as a more primitive primate member of the premonkeys or prosimians, see also Simons, 1971. Although its teeth and jaws are much smaller and of simpler structure than are those of *Parapithecus*, "*Qatrania*" should be placed in the Parapithecidae. The search for further

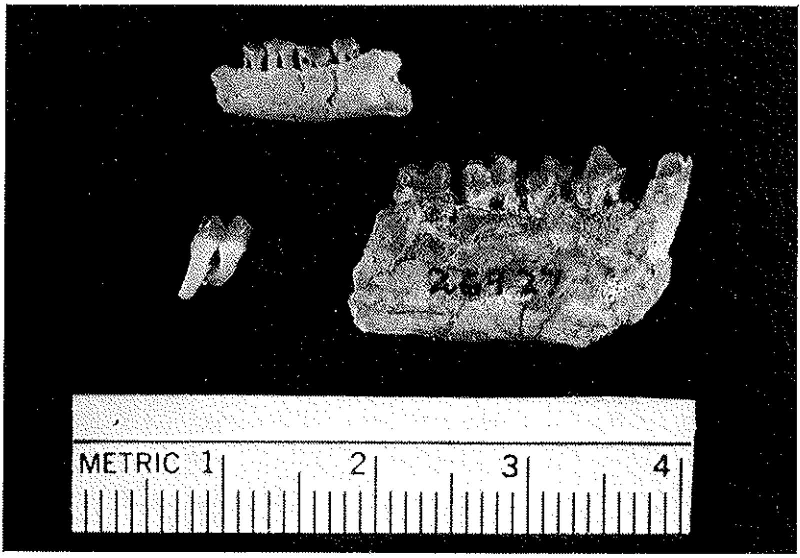


FIG. 1. The three known earliest African fossil Anthropoidea all recovered from Quarry E in the lower levels of the Jebel Qatrani Formation (Lower Fossil Wood Zone). Above: A new genus and species of parapithecid. Lower Right: The type and only mandibular specimen of *Oligopithecus savagei* found in 1961. Lower Left: A single molar of the same species found in 1980.

remains of these two species, as well as any other primate contemporaries they may have had, in the older Fayum Oligocene deposits remains one of the primary future exploration objectives of the Duke/Egyptian Survey research team now operating under my direction in Egypt each fall.

Today, the northern Fayum province of Egypt is a windswept desert, the Libyan Desert of Egypt. This wasteland is actually only the eastern edge of the great Sahara which sweeps westward unbroken for 4,000 kilometers to the Atlantic. In Oligocene times, some 35 million years ago, the same spot was a lush tropical lowland, watered by major rivers along whose banks grew a dense gallery forest. During many millions of years a geological section of rock was slowly built up that, in places, is more than 600 meters thick. In these deposits are two main series of river channel deposits, the Lower and the Upper Fossil Wood Zones. Of these, the lower zone is perhaps about 34 or 35 million years old, the upper approximately 28 or 29. As we have already discussed, only two primate jaws and a few isolated teeth have as yet been discovered in the lower zone. In the upper zone, fossil primate remains are so abundant that they are the commonest mammals occurring there. As we have already seen, these Upper Fossil Wood Zone primates belong to four genera. Of these four distinct genera each, save *Aegyptopithecus*, has two or more known species. The monkey-like genera were both described long ago — *Apidium* in Osborn, 1908 and *Parapithecus* in Schlosser, 1911 as was the ape *Propliopithecus*. I named *Oligopithecus* much later in Simons, 1967, and *Aegyptopithecus* in Simons, 1965. Species of two other genera, *Moeripithecus* and *Aeolopithecus*, have been transferred to *Propliopithecus*.

The Fayum parapithecids are of considerable interest for two main reasons: their greater abundance numerically has led to much more complete documentation of the entire postcranial skeleton. Other than those of Propliopithecidae, these postcranial elements are by far the oldest known for any Higher Primates. Secondly, their very presence as members of a quite distinct family in the African early Oligocene gives evidence of a much earlier split from the stock of the Fayum apelike primates. It is these propliopithecids which will be analyzed here first for they give us the earliest evidence as to the origin and primary features of the basal stem of our close relatives and ancestors, the group known as the hominoids: or apes together with men and pre-men.

Altogether quite distinct from each other as genera, the two apelike forms have usually been considered primitvie hominoids, the specific group of the apes and man, or have been ranked in a primitive taxonomic family, the Propliopithecidae, a group that had a larger snout, and less-developed tympanic tubes of the ears than later apes have had. The general structure of the molar teeth, particularly in *Aegyptopithecus*, is much like that of the *Dryopithecus*-group of Miocene apes. These latter chimpanzee-like creatures were first named in Lartet, 1856 from discoveries made in South Central France, and are only half as old as the propliopithecides. Of intermediate age between them are the earliest dryopithecines of genus or subgenus *Proconsul* (Hopwood, 1933) from the earliest Miocene of East Africa, found in several sites around the Kivarondo Gulf, Lake Victoria, Kenya and farther north in Uganda. *Aegyptopithecus* shows ancestral affinities to the *Proconsul* group in its tooth structure, for like *Proconsul*, its upper molars have well-developed shelves on the insides that hold a row of tiny bead-like cusps or "beaded cingulum". This is a shared primitive feature of these two early apes. The ape-like *propliopithecines* have never been found anywhere outside the Oligocene deposits of the Fayum, Egypt. At the top of the section of rocks in the

Fayum there is a lava flow. This basalt rock has been dated to an age of 25 million years. Because very extensive erosion had completely eroded away the whole 600 meter thick layer of Oligocene rocks in some places before this lava flow was laid down, we know that the age of the youngest specimens of *Aegyptopithecus* and *Propliopithecus* which come from about 80 meters below the basalt must be several million years older than 25, perhaps 28 or 29 million years old.

Early Discoveries

The first mandible of an ape to be discovered in the Fayum desert was a mandible recovered by a professional collector of fossils named Richard Markgraf. The specimen he found was sold to the Stuttgart Natural History Museum and was described in 1911 by Dr. Max Schlosser. This jaw, almost the size of that of a small modern lesser ape or gibbon, preserved parts of the front and both sides of the lower jaw. All the successive lower teeth were intact on one side or the other, except for the last front teeth or incisors. Markgraf left no record of the place or level in the Fayum where he found this specimen. Nevertheless, Dr. Schlosser gave it a description and a name in 1911 when he called the find *Propliopithecus haeckeli* in honor of the famous biologist. Nothing quite like this mandible — at least not the same species — has yet been found in the Fayum. Even so, almost exactly 50 years after *Propliopithecus* was named, my research group located some more single teeth of *Propliopithecus* at a new site I had found in 1961, Quarry G. This spot is just at the middle level of the Oligocene age deposits in the cliffs north of Lake Qarun.

Once it was described, *Propliopithecus* entered the textbooks as the world's oldest ape. After that first description no one ever questioned that it resembled both the group of the apes and that of man as well. Schlosser suggested that *Propliopithecus* might be related, on the one hand, to the ancestry of man, or alternatively, it might have been connected with the ancestry of the gibbon.

What was unusual about this first-found jaw of a Fayum ape-like form was that the two premolars (central teeth in the row between the canines and the molars) were about the same size and of a similar shape. Each of us (apes and humans) has two premolars on each side of each jaw. But in nearly all apes the front one, which we call premolar 3, is long and blade-like. In *Propliopithecus* it was not long and this was a resemblance to man and his relatives where both premolars are short and rounded. In the case when these two premolars (sometimes called bicuspids) are both short and rounded they are termed "homomorphic" or "same-formed". If the first of the pair is elongated, as in most apes and monkeys of the Old World, the premolars are termed "hetermorphic" or "different-formed". A long front premolar sharpens the back blade of large upper canines. When the front one of the two premolars is short, it correlates with relatively small upper canines.

The first fossil ape ever found *Pliopithecus antiquus* was described by a French scientist Lartet in 1837. We now know that females of this French Miocene species show homomorphic premolars and the teeth of this ancient ape of France closely resemble those of the Egyptian Oligocene ape. We may conclude that when Max Schlosser of Munich named this first-found Egyptian ape in 1911 he wanted to name it *Propliopithecus* in order to call attention to a relationship with the later French Miocene form. The term translates as "before-more-of an ape".

When young Markgraf discovered the unique type lower jaw of *Propliopithecus* a problem was raised that was not solved for a whole lifetime. Were the resemblances to humankind which this jaw showed due to its being a female whose mate would have had larger, apish front premolars or were the premolars homomorphic like man? With only the single specimen known, the problem could not be solved.

In 1959 I initiated a program of research in Egypt with the objective of finding out more about this oldest of the apes. It was obvious that without any knowledge of the upper jaws and teeth, or of the skull and skeleton, *Propliopithecus* would remain a mysterious animal. This research in Egypt falls into two parts, a period of seven expeditions I led, working from Yale University during the 1960s, and then at the end of the 1970s and in the early 1980s, five field seasons carried out from the Primate Center at Duke University.

When one searches for fossils the unexpected rather than the predictable is the rule. Rather than immediately finding more *Propliopithecus* the best specimens we located were of a different and larger ape to which, in 1965, I gave the name *Aegyptopithecus zeuxis* — the "connecting-Egyptian ape". There was another type of ape also recovered in the 1960s it was again represented by a sole lower jaw as had been the type of *Propliopithecus*. In the early 1960s, several different jaws of *Aegyptopithecus*, the commonest Oligocene ape, were discovered. The second unique lower jaw I called *Aeolopithecus chirobates*, Simons 1965.

Shortly after these animals were named, we discovered an almost complete ulna (see Fleagle, Simons and Conroy, 1975) and a skull of *Aegyptopithecus* in an upper level quarry: M. Meanwhile, a few more jaws as well as toe bones and tail bones we thought might belong to *Aegyptopithecus* turned up in our Quarry I at the same level as M. These and many later finds make it possible for us to recreate the probable appearance of *Aegyptopithecus.* Of particular importance is the skull of *Aegyptopithecus.* It is the only Old World Higher Primate skull we know of from anywhere throughout a huge — twenty million year long — slice of earth history. Between skulls of animals called *Adapis* in the late Eocene of France at about 45 million years of age and the skull of *Proconsul* apes in the early Miocene of Kenya (which lived some 18 million years ago) as far as the Old World is concerned, this skull of *Aegyptopithecus* is the only known fossil primate skull. The skull of *Aegyptopithecus* is a perfect example of what Charles Darwin first called a "connecting link". Combined uniquely in the skull are primitive features resembling those of European and North American Eocene primates and advanced conditions that group it with Miocene (and later) apes. Plates of bone surrounding the eye make up an "eyesocket" and the two separate frontal bones of lower primates are here fused along the mid-line to make up one frontal bone. Both these features are advanced features as in Old World apes, monkeys and men. Equally this skull shows ancient or primitive features. Two of these are: the very large premaxillary bones of this skull that look like those of Eocene prosimians and the external auditory tube of the ears, which in higher primates extends far outward of the auditory region but here is more primitive and ends at the margin of the auditory opening of the bulla, for further details and illustrations of this skull in Simons 1967, 1972.

Nature of New Discoveries

During the 1960s, techniques for finding Egyptian Oligocene fossils improved. The ancient deposits there are not hardened into rock, but even now are composed of loose sand and gravel. When the wind blows strong across the sands a sandblasting process cuts down into the sediments and exposes the fossils. The natural erosion can be sped up by sweeping away an overlying layer of accumulated hard rock fragments made up of bits of quartz, chert, bog iron, lava, and silicified wood. In English this layer or crust on the desert is called "desert pavement". At the end of each year's expedition our cooperating team of American and Egyptian scientists spend several weeks sweeping off this desert pavement so that by the time of the following year's research many new fossils will have been exposed. The large areas now exposed have been harvested very successfully in the last five years to produce a much higher rate of recovery of important fossils than was possible in the 1960s.

Before 1977 only about seven relatively complete ape-like jaws had been accumulated, these were the type *Propliopithecus*, *Aeolopithecus*, and five of *Aegyptopithecus*. Now in the last five seasons about thirty more good jaws have been found. A half dozen of these were of *Propliopithecus* but they are not the same as the type species, they are larger and different in detail. They do show something else: that the creatures Schlosser in 1911 called *Moeripithecus* and the one I had named *Aeolopithecus* in 1965 are both actually species of *Propliopithecus*, see Kay, Fleagle, and Simons, 1981. So the one from the upper zone should now be called *Propliopithecus chirobates*. Much more significant than these taxonomic details, however, is the fact that all these newly recovered jaws of both *Aegyptopithecus* and *Propliopithecus* make it possible to study populations, and with this possibility available it was determined that both these kinds of early apes had marked differences in canine and front premolar size between the sexes. The social organization in primates is different among animals that have different-sized sexes and so the new material for the first time has allowed speculation as to ancient catarrhine social organization, see Fleagle, Kay, and Simons, 1980.

Perhaps the most striking implication to be derived from these new sexually distinct finds of *Propliopithecus chirobates* is that the sole original mandible found by Richard Markgraf is a female and by analogy with the other species of the genus would have had males with more heteromorphic premolars like apes, not humans. This removes *Propliopithecus* from serious consideration as a human forebear, (as was originally implied as one possibility by Schlosser) in preference to its contemporary *Aegyptopithecus*. Because of the distinct resemblances, not seen in *Propliopithecus* between *Aegyptopithecus* and the later Miocene group of dryopithecines I have long considered *Aegyptopithecus* our more probable Oligocene ancestor. In addition to the many new jaws the expeditions of 1977 produced four distal humeral fragments of apes which were described in Fleagle and Simons, 1978. Then in 1980 two nearly complete humeri of *Aegyptopithecus* were found, one each in quarries I and M, Fleagle and Simons, 1982. When taken together with ulna found in 1966, these forelinmb bones provide the main scientific evidence about the manner of locomotion of our Oligocene ancestors.

Relationships Between the Propliopithecids

Aegyptopithecus and *Propliopithecus* differ in several ways that are instructive, not only in determining their places in the primate family tree but for determining their lifestyles as well. Most of the fossils of both *Aegyptopithecus* and *Propliopithecus* come from the upper part of the badlands (Upper Fossil Wood Zone). Thus they are largely contemporaries. It seems unlikely that one genus is ancestral to the other. The one exception may be the very first jaw found by Markgraf, *Propliopithecus haeckeli,* which we think is older than the other two species: *Propliopithecus chirobates* and *Aegyptopithecus zeuxis.* Species of the two genera must have had different diets for their tooth proportions and structures are just as distinct as are those of the genera of living apes. *Propliopithecus* may have been specialized to break open and eat softer fruits and buds than *Aegyptopithecus*, for it has relatively larger front teeth (incisors) and big premolars while its molars have the distinctly smaller molar area typical of frugivores. In *Aegyptopithecus*, in contrast, the premolars and incisors are comparatively smaller and the molars are large and increase in size to the rear. This larger molar area would make powerful chewing easier, so perhaps, *Aegyptopithecus* opened and chewed tough-skinned fruits or nuts. Their possible diet, ecology, and dental morphology are reviewed in much more detail in Kay, 1977 and Kay and Simons, 1980. The molars of *Propliopithecus* usually have more laterally placed cusps and upper cheek teeth are broader across than in *Aegyptopithecus*, see Kay, Fleagle and Simons, 1981. In teeth of the latter genus also, there are pronounced shelves, or cingula, on the insides of upper premolars and molars. As already pointed out, on these shelves are many small cusps — arranged like a string of beads. Consequently, they are called "beaded-cingula". Such cingula make *Aegyptopithecus* resemble closely the more recent Miocene apes of Kenya and Uganda called *Proconsul,* but as would be expected for a much older animal the upper cheek teeth are shorter from front to back. *Proconsul* is widely accepted as the basal member of a group of fairly large mid-Tertiary apes, the dryopithecines from which nearly all scientists concerned with human origins believe both the modern great apes and man descend. The first of this group to come to the attention of scientists was *Dryopithecus fontani* found at Saint Gaudens in southern France and named by Lartet in 1856. Structural resemblances between the teeth of *Aegyptopithecus* and the dryopithecines put it in or near the base of the dryopithecine group and this in turn places it in or near our own ancestry. *Dryos*, meaning "oak", was used by Lartet because oak leaves occurred in French Miocene deposits similar in age to the first-found *Dryopithecus* fossils. The relationships of *Propliopithecus* are perhaps more obscure although it is probably still a good bet that it is related to *Pliopithecus* or *Epipliopithecus* from the Miocene of France and Czechoslovakia as was originally suggested by Schlosser in 1911. We have seen that although it is related to *Aegyptopithecus*, teeth indicate that *Propliopithecus* was not eating the same thing, their lifestyles were different. The small laterally placed molar cusps and the similar-sized first, second, and third molars make *Propliopithecus* look more like a second group of smaller East African Miocene apes, sometimes called the limnopithecines which have been ranked with the modern gibbon and siamang — the lesser apes of southeast Asia.

Should these relationships be confirmed then it would appear that two major groups of apes had already become separately definable stocks by about 28 million years ago when the two kinds of Fayum ape-like forms lived. An alternate theory is that *Propliopithecus* and the European *Pliopithecus* group are not related to gibbons but represent an extinct side branch. As is well detailed in other contributions to this conference, some scientists have tried to determine numbers in millions of years for the split points or branching times in the ancestry of the various primates and other vertebrates. A split-point can be defined as the date when two groups split from a common ancestor. To arrive at these dates biochemists measure the amount of immunological, or other chemical, difference between two primates and convert this into a time estimate on the assumption that one or another date of branching among primates is known from the fossil record and that the rate of change of biochemical substances in all lineages has progressed at the same rate. Only with these two assumptions confirmed could the so-called molecular "clock" be made to work. However, paleontologists know almost nothing about when the first branching leading to any two groups of the modern (biochemically testable) primates occurred. Likewise many evolutionary biologists have challenged the assumption that chemical evolution proceeds at constant rates. In any case the molecular clock date, derived as we have seen from the amounts of chemical difference existing between any two living groups, in the case here, the greater and the lesser apes, would put the split-point nearer the present time. Although some of these scientists believe that the molecular distance data puts the split-point between these two main groups of apes at only about 18 million years, others conclude that the gibbon group and the great ape group were already distinct at 20-22 million. Should *Propliopithecus* be an evidence that this branching had already happened in the Oligocene then the split would be even earlier, say 26 to 28 million.

Lifestyle of the Parapithecids

The parapithecids from the Fayum can definitely be considered to have reached the monkey grade of organization for they show fused mandibular symphysis, postorbital closure, and a closed metopic suture of the frontal as do all Anthropoidea. Gingerich, 1973, attempted to demonstrate a pre-anthropoidean condition of the tympanic region for *Apidium* but Cartmill, MacPhee, and Simons, 1981 have shown that the squamosal fragment attributed by him is definitely not of a primate but perhaps of a hyaenodontid creodont, *Masrasector*. Thus, the ear region of Parapithecidae is not known to differ from that of propliopithecids. Although I do not believe that the dental, cranial, and postcranial anatomy of parapithecids is particularly like that of the New World monkeys, these early African catarrhines do share many primitive or lemur-like features with the platyrrhines together with a few details of the pelvis (such as the arrangement of sacral, gluteal, and iliac planes) resembling that of Cercopithecoidea and Hominoidea.

As now best understood, the parapithecids can be interpreted postcranially as showing an overall adaptation unlike that of the Miocene-Recent cercopithecoid monkeys. Whether this adaptation could be converted into the locomotor system seen in the relatively recent cercopithecoid radiation is anyone's guess. The interpretation of the hindlimb of *Apidium*, to which most known fore, and hindlimb bones of parapithecids belong, is that it shows extreme locomotor adaptations to quadrupedal leaping not seen in extant higher primates, but it may be in some way like what the ancestors of *Tarsius* might have been before their extreme limb specialization and tibiofibular fusion. *Apidium* shows, for example, a tibiofibular syndesmosis extending nearly one-third of the distance up the lower leg which effectively restricts the ankle to a hinge joint. *Apidium* is therefore much committed to leaping. It is an unfortunate coincidence that we know best the forelimb of Propliopithecidae and the hindlimb of Parapithecidae. This of itself limits comparison of the two families, although ulna and humeri of both seem at about the same adaptive grade.

The distinctive hindlimb of *Apidium* may set this group apart from the ancestry of cercopithecoid monkeys, but it should be remembered that many mandibula and dental affinities exist between the small living cercopithecoid, *Cercopithecus talapoin* and the species *Parapithecus grangeri* from the Fayum, see Simons 1967, 1974.

Lifestyle of the Propliopithecids

Judging from the size of known parts we can deduce that *Aegyptopithecus* was about the size of a house-cat with a probable weight of 10-12 pounds. *Propliopithecus* species were distinctly smaller probably weigbing about 6-8 pounds. Weights must have differed significantly between the sexes as well for we know that species of both these genera had sexes with different-sized canines and jaws. This in turn, by analogy with nearly all diving primate species, indicates that the propliopithecids had large multimale/multifemale social groups. By late Oligocene times, inter-individual recognition and competition had become a more important factor in the context of a large social group, see Fleagle, Kay, and Simons, 1980.

When the Fayum Oligocene fossil beds were being deposited the principal process was overbank and river channel sedimentation at what are called point-bar deposits, see Bown, 1981. Thus, all skeletons and limb bones became scattered and broken, almost never are any two different bones deposited together. Because of this damage we have few parts of the limb-skeleton of propliopithecids from which to judge their principal methods of climbing and leaping. We think also that, after death, many of these ape- and monkey-like primates were eaten by catfish, turtles, and crocodiles. All these animals swarmed in the ancient Fayum rivers, as the high frequency of their own bones preserved in the Fayum gives evidence.

The nearly complete forelimb bones and few foot bones that have been recovered for *Aegyptopithecus* indicate that it was a rohust and comparatively deliberate arboreal quadruped that did not habitually swing under branches as modern apes do. Rather, like the howling monkeys of South America, it presumably walked and ran about on top of the branches. This suggests that rapid leaping and climbing would have been difficult and infrequent. The distal articular region of the humerus is at about the structural level of many living S. American monkeys or *Pliopithecus* from the European Miocene. Fleagle and Simons, 1982 show that the proximal portions of the two newly recovered *Aegyptopithecus* humeri have many features that resemble Eocene and Recent prosimians and that are lost in all living Old World Anthropoidea. This, in turn, suggests that in many features *Aegyptopithecus* might be more primitive than the condition posited for a last common hominoid-cercopithecoid ancestor. Fleagle and Simons, 1982, support the view that propliopithecids could have been ancestral to both Hominoidea and Cercopithecoidea.

As we have seen already, the construction of the dentition of the two propliopithecids may be used both to distinguish them and to relate them to other forms. These tooth-structures also provide information about diet because we know that relatively flat tooth structure without tall, pointed cusps goes along with the eating of herbaceous foods, fruits, nuts, and the like, rather than meat. In sum, *Aegyptopithecus* with larger hack teeth might have been eating tougher food items while the comparatively larger incisors of *Propliopithecus* could have been for scooping out fruit much as the modern South American saki and howling monkeys do.

Considering shape of face and head, we know a lot about *Aegyptopithecus* but have practically no information about *Propliopithecus*. This is because a skull of *Aegyptopithecus* as well as many lower jaws have been found. In 1981, a second partial skull which consists of a very well preserved facial region was discovered. It is an old male while the find of 1967 was a subadult male. The two faces are extremely different, see figure 2. The snout of *Aegyptopithecus* was large and long and it had a rather small brain relative to modern Higher Primates. For its time the brain structure, which can be calculated from endocranial moulding, seemed to be advanced, Radinsky, 1973. Night-time active primates have very large eyes, like owls, and daytime active forms show smaller eyes. *Aegyptopithecus* is like the latter: the skull across the eyes is about 5 cm broad while total skull length is about 10 cm. It would seem that *Aegyptopithecus* was an animal in which vision had become increasingly important and whose activities, feeding on fruit and fresh vegetative growth took place in the day. A final detail about the way of life of *Aegyptopithecus* derives from the large sample of over a dozen apes found in the last five years. We have seen that the canine size and front premolar size differs greatly between the sexes of both *Aegyptopithecus* and *Propliopithecus*. Especially in *Aegyptopithecus* the mandibles of males are much more robust with strongly developed ridges for muscular

FIG. 2. Comparison of the facial skeleton in *Aegyptopithecus zeuxis* from Quarry M, Jebel Qatrani Formation upper levels (Upper Fossil Wood Zone), Fayum Province, Egypt. Left: Facial view of 1967 skull of subadult male (incisors restored). Right: Facial view of fully adult male discovered in November 1982.

attachment. Thus the sexes of dawn apes clearly different both in canine size and in body size. What is most remarkable here in making inferences about the past is the correlation between the amount of dimorphism exhibited by a primate species and its typical social organization. Those species where individuals live alone much of the time or bonded in pairs usually have similar-sized sexes in which canines are of subequal length between them. On the other hand, as we have seen, larger groups with multiple males and females, a polygynous social group, is typified among living primates by a marked difference in canine and jaw size between the sexes. Such groups, because they require the individual member to learn to identify many individuals as troop members, provide a context which would select for greater intelligence and the ability to cooperate with and communicate with other species members. These behavioral features, together with prolongation of the learning period in infancy and childhood would go far to explain why strong selection for intelligence characterized this particular group of mammals. As we all know the selection process has culminated in the production of *Homo sapiens.*

In conclusion, scholars can now say that the earliest presently known forerunners of the apes and man were dwellers in the tropical forests of north Africa 25 to 35 million years ago. All postcranial features detailed so far for both *Apidium* and *Aegyptopithecus* confirm their arboreality, see Fleagle in Bown et al., 1982 (in press). Thus, in the story of human descent it is still true that arboreal living preceded for many millions of years the descent to the ground. It is important to stress this point for Kortlandt (1980) has recently proposed that the Fayum environment was that of a dry grassland or semiarid sahalin and that its primates were therefore terrestrial. Bown et al. (1982) constitutes a reply to Kortlandt's argument. This contribution shows from a variety of scientific lines of evidence that his hypothesis of a relatively arid Fayum is without basis. Trace fossils, fossil plants, the fossil vertebrates as a whole, and both old and new sedimentological and paleopedological evidence all combine to indicate that in Oligocene times, the Fayum evidently was sub-tropical to tropical. Fossils were buried on a low lying coastal plain where abundant tall trees, vines, and local mangroves grew. Soils were largely damp and seasonal fluctuations in rainfall occurred. In 1981, S. L. Wing conducted a new paleobotanical survey of the Fayum. His preliminary conclusions (written communication, 1981) are as follows:

> The floristic affinities of the fruits, seeds, and leaves of the Jebel Qatrani Formation are strong evidence that the Oligocene vegetation includes areas of brackish and freshwater marsh as well as stands of tropical forest. The diversity of lianes and vines, in addition to the climatic requirements of Araceae, Sterculiaceae, and members of the Annonaceae, suggest that this forest grew under a climate no drier than monsoonal.

Thus, it is clear that all lines of evidence put the earliest hominoid ancestors in the tropical forest environment. In fact, the commonest fossil fruit from the Jebel Qatrani Formation *Epiprimnum* (family Araceae) may well have been eaten by *Apidium* and *Aegyptopithecus* alike. It is known that the fruits of certain modern day Araceae are eaten by both macaque and man.

REFERENCES

BOWN T. M. and KRAUS M. J., *Fayum's Jebel Qatrani Formation (Oligocene) is fluvial.* « The Cross-Section (U. S. Geological Survey) », *14*, 11-13 (1981).

BOWN T. M., KRAUS M. J., WING S. L., TIFFNEY B. G., FLEAGLE J. G., SIMONS E. L. and VONDRA C. F., *The Fayum Primate Forest Revisited.* Submitted to « Journal of Human Evolution », (1982, in press).

CARTMILL M., MACPHEE R. D. E. and SIMONS E. L., *Anatomy of the Temporal Bone in Early Anthropoids, with Remarks on the Problem of Anthropoid Origins.* « American Journal of Physical Anthropology », *56*, 3-21 (1981).

FLEAGLE J. G., KAY R. F. and SIMONS E. L., *Sexual Dimorphism in Early Anthropoids.* « Nature », *287*, 328-331 (1980).

FLEAGLE J.G. and SIMONS E.L., *Humeral Morphology of the Earliest Apes.* « Nature », *273*, 705-707 (1978).

FLEAGLE J. G. and SIMONS E. L., *Skeletal Remains of* Propliopithecus chirobates *from the Egyptian Oligocene.* Submitted to « Folia primatologica », (1982a, in press).

FLEAGLE J. G. and SIMONS E. L., *The Humerus of* Aegyptopithecus zeuxis, *a Primitive Anthropoid.* Submitted to « American Journal of Physical Anthropology », (1982b, in press).

FLEAGLE J. G., SIMONS E. L. and CONROY G., *Ape Limbbone from the Oligocene of Egypt.* « Science », *189*, 135-137 (1975).

GINGERICH P. D., *Anatomy of the Temporal Bone in the Oligocene Anthropoid* Apidium *and the Origin of the Anthropoidea.* « Folia primatologica », *19*, 329-337 (1973).

HOPWOOD A. T., *Miocene Primates from Kenya.* « Journal of the Linn. Soc. (Zool.) », *38*, 437-464 (1933).

KAY R. F., *The Evolution of Molar Occlusion in the Cercopithecidae and Early Catarrhines.* « American Journal of Physical Anthropology », *46*, 327-352 (1977).

KAY R. F., FLEAGLE J. G. and SIMONS E. L., *A Revision of the Oligocene Apes of the Fayum Province, Egypt.* « American Journal of Physical Anthropology », *55*, 293-322 (1981).

KAY R. F. and SIMONS E. L., *The Ecology of Oligocene African Anthropoids.* « International Journal of Primatology », *1*, 21-37 (1980).

KORTLANDT A., *The Fayum Primate Forest: Did it Exist?* « Journal of Human Evolution », *9*, 277-297 (1980).

LARTET E., *Nouvelles observations sur une macboire inférieure fossile, crue, d'un singe voisin du Gibbon, et sur quelques dents des ossements attribués a d'autres quadrumanes.* « C. R. Acad. Sci. », *4*, 85-93 (1837).

LARTET E., *Note sur un grand singe fossile qui se rattache au groupe des singes supérieurs.* « C. R. Acad. Sci. », *43* (1856).

OSBORN H. F., *New Fossil Mammals from the Fayum Oligocene.* « Bulletin of the American Museum of Natural History », *24*, 265-272 (1908).

RADINSKY L., Aegyptopithecus *Endocasts: Oldest Record of a Pongid Brain.* « American Journal of Physical Anthropology », *39*, 239-248 (1973).

SCHLOSSER M., *Beiträge zur Kenntnis der Oligozanen Landsäugetiere aus dem Fayum, Agypten.* « Beitr. Paleontol. Geol. Ost. Ung. », *24*, Vienna (1911).

SIMONS E. L., *Two New Primate Species from the African Oligocene.* « Postilla », *64*, 1-12 (1962).

SIMONS E. L., *New Fossil Apes from Egypt and the Initial Differentiation of the Hominoidea.* « Nature », *205*, 135-139 (1965).

SIMONS E. L., *The Earliest Apes.* « Scientific American », *217*, 28-35 (1967).

SIMONS E. L., *Relationships of* Amphipithecus *and* Oligopithecus. « Nature », *232*, 489-491 (1971).

SIMONS E. L., *Primate Evolution.* New York: Macmillan Co. (1972).

SIMONS E. L., Parapithecus grangeri (*Parapithecidae, Old World Higher Primates*): *New Species from the Oligocene of Egypt and the Initial Differentiation of the Cercopithecoidea.* « Postilla », *166*, 1-12 (1974).

SIMONS E. L. and KAY R. F., *Description of a New Oligocene Primate from the Fayum Province of Egypt*: Quatrani wingi (1982, in preparation).

RECENT ADVANCES AND SUGGESTIONS FOR EXPANSION OF THE FIELD OF HUMAN ORIGINS

LEONARD O. GREENFIELD
Department of Anthropology Temple University
Philadelphia, U.S.A.

Recent advances

In the past five years there have been substantial changes in the interpretation of ape and human ancestry. This is especially true in the area concerning the origins of the lineages leading respectively to each of the extant great apes and man. From the early 60's to the late 70's the major paleontological current of opinion was that "*Ramapithecus*" represented the earliest hominid and a divergence between our lineage and the lineages leading to the extant great apes, *Pan*, *Pongo*, and *Gorilla*, must have occurred sometime in the Early Miocene or Late Oligocene. "*Ramapithecus*" was perceived to have, among numerous dryopithecine species, unique adaptations which foreshadowed the *Australopithecus* condition [1].

Necessarily following from this interpretation of the fossil evidence was the conclusion that the extant great apes and man were derived from a last common ancestor which lacked many of their shared characteristics. Thus, this early divergence hypothesis relied heavily on the phenomenon of independent acquistion to account for the origin of those derived characteristics shared by the extant great apes and man and supported the prebrachiationist concept of ape/human origins rather than the brachiation-knuckle walking theory which is based largely upon phenetic evidence [2-4].

This early divergence hypothesis was supported almost entirely by the claims about "*Ramapithecus*" [5]. When it became apparent that contemporary Middle Miocene dryopithecines like *Sivapithecus* were virtually indistinguishable from "*Ramapithecus*" [6-10] the early divergence hypothesis was modified [11]. Thick and thin molar enamel, rather than "*Ramapithecus*", became the pivotal adaptation (or marker) in the divergence of pongids and hominids. However, like the "*Ramapithecus*" hypothesis, it was also necessary to cite the same amount of independent acquisition to explain the origin of derived characteristics shared by the extant great apes and man [5].

The early divergence hypothesis based on thick vs. thin enamel has proved to be weak in other ways [5]. First, the "thick" enameled forms show a wide range of variation in enamel thickness which appears to be, among dryopithecines, a continuous variable which does not sort dryopithecines neatly into two discrete classes. Second, it does not sort the extant descendants into two classes. Both *Pongo* and *Australopithecus*/*Homo* [12-13] have thick molar enamel and it was conceivable to Gregory and Hellman [14] and others [10, 15] that, on the basis of dental and gnathic adaptations, *Pongo* could easily be derived from one of the Asian *Sivapithecus* species (thick enameled forms). This now seems almost a certainty with the discovery and publication [16] of the new face of *Sivapithecus* from Pakistan which shows many general and specific resemblances to *Pongo*. In fact, regardless of its other weaknesses, a relationship between *Pongo* and *Sivapithecus* falsifies the thick and thin molar enamel hypothesis because the hypothesis predicted that none of the thick enameled forms would be ancestral to any of the extant great apes. And, last, the major reason thick and thin enamel was cited as a pivotal point of divergence between human and great ape lineages was because the difference was supposed to be related to the onset of a divergence in lifestyles. It was suggested [17-18] that thick molar enamel was indicative of more hominid-like ground feeding with associated high attrition rate diets, while thin enamel was related to arboreal feeding with associated low attrition rate diets. However, Kay [13] found that thick enamel is not associated with ground feeding; terrestrial or arboreal extant primates with thick molar enamel feed on hard nuts. This finding suggests that thick molar enamel is probably not an adaptation which delays the effects of attrition from gritty foods obtained in terrestrial feeding, but, rather, it is more likely an adaptation which resists occlusal stresses created by powerful vertical compression. Thus there is much less reason to argue that thicker molar enamel should be regarded as a pivotal adaptation or marker in the divergence of the great ape and human lineages. Thus, by the end of the 70's, there were serious doubts about the accuracy of the two major paleontological hypotheses.

Paleontologists were not the only scientists investigating ape and human ancestry in the last two decades. Beginning in the late 60's another school of thought came to conclusions [19-23] about human and great ape phylogeny which were mutually exclusive of the conclusions derived from paleontological evidence. In these phenetic studies, especially those using characters of simple inheritence (proteins) or DNA itself (hybridization), two major differences with the paleontological school arose.

First, based on estimates of rates of change in proteins and other assumptions [24], serologists derived divergence date estimates that were far less than the 20-25 million year estimates of paleontologists. A date of 5 million years for the divergence of the *Pan*, *Gorilla* and *Homo* lineages, based on serology, excluded the possibility that *"Ramapithecus"* could be the earliest representative of the lineage leading to *Australopithecus* and *Homo.* This glaring contradiction, which seemed unresolvable, led each school to reject the data and conclusions of the other and blocked a synthesis of all relevant data.

A second important difference in interpretation, although a more subtle one, involved the number of branching events. Traditionally, paleontologists sought a single branching event between the extant great apes and man. This phylogenetic interpretation and the notion that the lifestyles of the extant great apes are more similar to each other than any is to man's were reflected in a taxonomic scheme which included *Pan*, *Gorilla*, and *Pongo* in the Pongidae and "*Ramapithecus*" (generally) and *Australopithecus* and *Homo* in Hominidae. On the other hand, serologists and those studying DNA hybridization concluded that there were two branching events (fig. 1) and that *Pan*, *Gorilla* and *Homo* were more closely related to each other (and about equally) than any was to *Pongo*. On the basis of this phenetic evidence, Goodman [19], for example, lumped all the extant great apes and man in Hominidae and further set up two subfamilies: Ponginae (including *Pongo*) and Homininae (including *Pan*, *Gorilla* and *Homo*).

In order to resolve the differences between the two schools of thought, a late divergence hypothesis was proposed [5, 10]. The late divergence hypothesis was the result of a new interpretation of the pale-

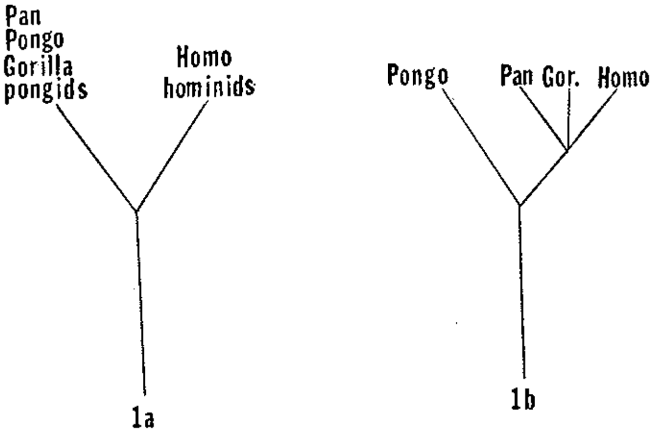


FIG. 1

ontological evidence and a more synthetic approach to phylogenetic reconstruction.

As noted above, recent work on "*Ramapithecus*" [6-9] showed that the taxon's dental and gnathic adaptations were not unique. Systematic comparisons between "*Ramapithecus*" and all relevant hominoid taxa indicated "*Ramapithecus*" was a small version of *Sivapithecus*. The few real differences between the "*Ramapithecus*" species and other Sivapithecus species (relative canine size, facial prognathism) are most likely related to allometric scaling (the different species are functional equivalents at varying sizes).

It was further argued that the genus *Sivapithecus* might also include other specimens assigned to "*Ouranopithecus*", "*Bodvapithecus*", "*Rudapithecus*" (although I now would not place these specimens into *Sivapithecus*), "*Ankarapithecus*", "*Graecopithecus*" *D. keivuanensis* and the Candir and Pasalar specimens. They are morphologically similar, probably part of the same adaptive radiation because they share very similar derived traits, and they exhibit similar dental and gnathic adaptations. These are the major reasons why congeneric status might be adopted by a consensus of workers.

What are the known adaptations of the genus *Sivapithecus*? Dental and gnathic features suggest *Sivapithecus* was a dietary generalist (omnivore) because the taxon lacked specializations associated with frugivory, folivory, and small object feeding [9, 25-26]. Most *Sivapithecus* species display adaptations, expressed in varying degrees, for powerful vertical compression. Wolpoff [27] has suggested that the adaptations to powerful vertical compression would have extended the range of dietary items that *Sivapithecus* could have masticated and were the basis for adaptive radiation. As dietary generalists, *Sivapithecus* species (unlike other dryopithecine species) were apparently able to exploit a wide range of ecological zones including tropical rainforests, woodlands, and open country habitats and some are believed to have lived in temperate zones. Also suggestive of this ability to masticate a wide range of dietary items is the observation (still unquantified) that despite a wide ecological, temporal and geographic range there is little morphological variation (in dental systems) among *Sivapithecus* species. Living and extinct baboon taxa, for example, exhibit a much wider morphological range (presumably because they possess more specialized dietary adaptations).

If *Sivapithecus* was a dietary generalist one might expect it to have exhibited a wide range of feeding behaviors. An expanded neocortex would have provided the neurological basis for an increased capacity to realize a wider range of learned behaviors. A hallmark of the extant great apes and man is greater mentation than is seen in other extant primates. It could be reasoned therefore, that their most likely last common ancestor [5, 10], *Sivapithecus*, was also of the same grade. This hypothesis will be tested as new cranial materials will reveal estimates of brain volume/ body mass proportions and whether *Sivapithecus* possessed the external neocortical features (as seen in endocasts) shared uniquely by the extant great apes and man.

Other systematic comparisons of *Sivapithecus* with related hominoids showed that its C/P_3 complex was fully ape-like and that among the numerous dryopithecine species it exhibited the greatest number of features which might be expected in a last common ancestor of the extant great apes and man (and the most appropriate geographic range for a last common ancestor). And, finally, given the dietary reconstruction and the ecological and metric range of the included species, it is also probable that the genus included forms that were both arboreal and terrestrial in varying degrees.

In addition to this reassessment of the Miocene hominoids, the late divergence hypothesis included information derived from the recently described specimens of *Australopithecus afarensis*, a Pliocene biped with a transitional dentition and *Pan*-sized cranial capacity [28-30]. The dental and gnathic morphology of *A. afarensis* showed that many unique human dental and gnathic traits did not evolve until after the Miocene [10] rather than by the Middle Miocene as was indicated by earlier interpretations of "*Ramapithecus*". It was also assumed in the late divergence hypothesis that the phenetic phylogeny (fig. 1b) was correct; that there were two branching points in the phylogeny of the extant great apes and man and that *Pan*, *Gorilla*, and *Homo* were more closely related to each other than any was to *Pongo*.

The major components of the late divergence hypothesis can be summarized briefly (fig. 2). On the basis of parsimony, *Sivapithecus* is the most likely last common ancestor of the extant great apes and man and makes its first appearance approximately 15 million years ago [31]. Asian species of the genus gave rise to *Pongo* and *Gigantopithecus*. The separation of the *Pongo* lineage can probably be extended back to the beginning of the Asian fossil samples (Chinji-12 mya) because dentally these specimens are very similar to the teeth associated with the recently published face which dates to 8 million years ago [16].

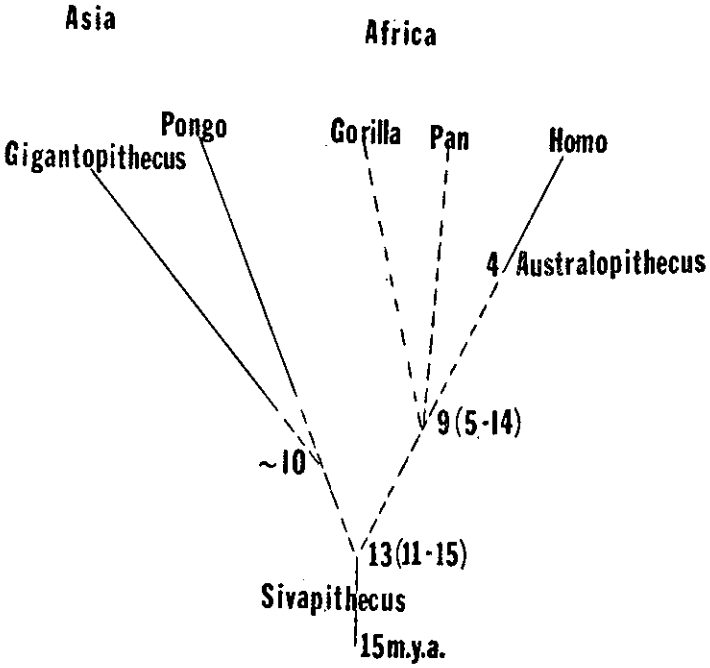


FIG. 2

and they lack cingula [10]. Thus the first branching point could be anywhere from 15-12 million years ago. The second branching point is still more difficult to pinpoint. It could be anywhere from 14-6 million years ago and probably was an African event. If the *Pongo* lineage split 12 million years ago the *Pan, Gorilla, Homo* split would date between 11 and 6 million years ago. The last common ancestor of *Pan, Gorilla* and *Australopithecus* most probably had low-moderate frequencies of molar cingula, a deep face with a deep palate and high zygomatic arches, a guttered nasal aperture, rounder orbits and a wider inter orbital breadth than Asian *Sivapithecus* or *Pongo*, suspensory locomotor adaptations, and a large brain volume/body mass proportion. Enamel thickness could have been as thick as it is in Asian *Sivapithecus* or thinner. If it was thick then reduction in enamel thickness in *Gorilla* might be explained as an adaptation to folivory — exposed dentin and alternating enamel/dentin/enamel surfaces might contribute to more effective shredding of herbivorous materials. The reduction of enamel thickness in *Pan* might be explained as structural reduction associated with frugivory along with the decrease in tooth size/body mass proportions.

As noted earlier, the late divergence hypothesis was the result of a reconsideration of the paleontological evidence and a synthetic method of phylogenetic reconstruction which, for reasons stated below, includes both phenetic and stratophenetic evidence. This method, which could be called panphenetic, weights the data used in phylogenetic reconstruction in the following order from greatest to least weight: phenetic data from characteristics of simple inheritence (proteins) and DNA hybridization, phenetic data from characteristics of complex inheritence (polygenic characters), and stratophenetic data (also polygenic characters). As a reflection of the reliability of the different forms of data, a phenetic phylogeny is derived first (just the branching events and not estimates of divergence dates) and stratophenetic data is filled in using the principle of parsimony.

The weighting of the various kinds of data is based upon how accurately each reflects the genetic differences and similarities between taxa. DNA hybridization and protein data are the most accurate indicators of relatedness. Polygenic characteristics of fossils are the least accurate and most ambiguous. However, while phenetic data more certainly measures differences in genotypes between *living* descendants it cannot be used to estimate divergence dates [24] nor trends of emergence as the stratophenetic data can. Thus both forms of data contribute to the *development* of phylogenetic scenarios. These scenarios make predictions which can then be *tested* by new stratophenetic evidence which is the ultimate source of phylogenetic information [32]. For obvious reasons, panphenetic methodology can only be applied to those sets of organisms which have both living and fossil representatives (the more the better).

The same procedure can be applied to a very similar set of problems which confront workers trying to determine the phylogenetic history of all primates. At present the major issue at stake concerns the origin of the anthropoids and two mutually exclusive positions have been supported [33-34]. Primarily on the basis of phenetic evidence, which shows that tarsiers are more closely related to anthropoids than are lemurs and lorises [19], omomyids are considered to be ancestral to tarsiers and anthropoids while adapids are considered to be the ancestors of lemurs and lorises (fig. 3). The other position, stated most recently by Gingerich [34], is supported primarily by good stratophenetic arguments (fig. 4). Omomyids are placed in an ancestral position to tarsiers while adapids are considered to be ancestors of anthropoids and lemurs and lorises.

The primary weakness of the scenario which places omomyids in

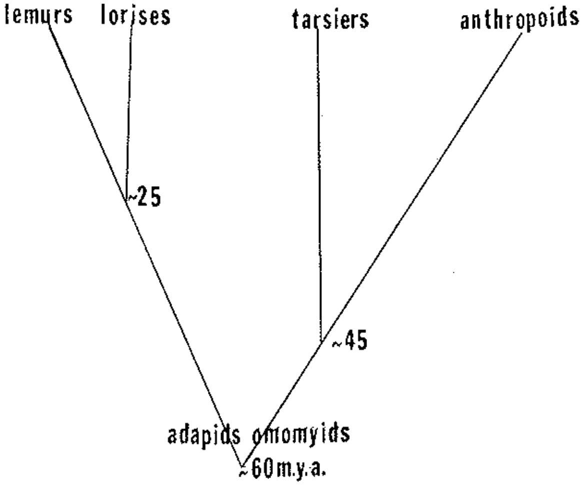


FIG. 3

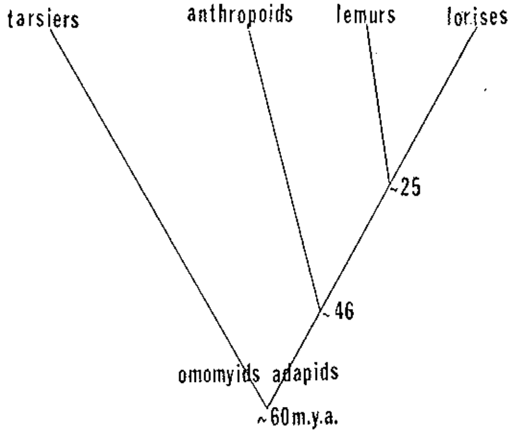


FIG. 4

an ancestral position to anthropoids is the lack of any good stratophenetic evidence; none of the known omomyids makes a credible ancestor of anthropoids. The primary weakness of the scenario which places adapids in an ancestral position to anthropoids and lemurs and lorises is that it contradicts the phenetic evidence which shows that tarsiers are more closely related to anthropoids than are lemurs and lorises. More workers have supported the omomyid scenario because they are more willing to contradict stratophenetic evidence than phenetic evidence.

By using the best arguments from both sides and examining the weaknesses of each one can arrive at a panphenetic phylogeny which offers one solution to the problem. First, a phenetic phylogeny is taken as a basis for the entire scenario (figs. 5, 6). The strongest stratophenetic evidence is now filled in without contradicting the phenetic evidence. Omomyids are placed as ancestors of living tarsiers — a relationship which both sides support. Next, following Gingerich's strong stratophenetic arguments, adapids are placed in an ancestral position to anthropoids. The last common ancestor of omomyids and adapids is placed in the Middle-Late Paleocene. However, in the panphenetic phylogeny, adapids are not placed in an ancestral position to lemurs and lorises. The stratophenetic arguments in favor of a relationship here are about as weak as the stratophenetic arguments in favor of an omomyid ancestry for anthropoids. Adapids, if ancestral to lemurs and lorises would have to have lost a wide range of anthropoid-like derived traits including spa-

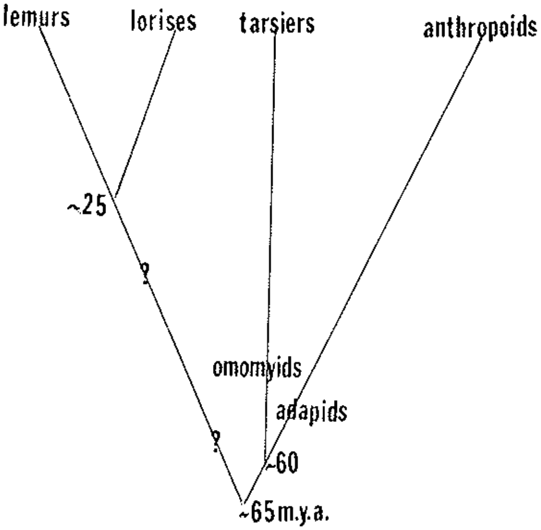

lemurs
lorises
tarsiers
anthropoids
~25
?
omomyids
adapids
?
~60
~65 m.y.a.

FIG. 5

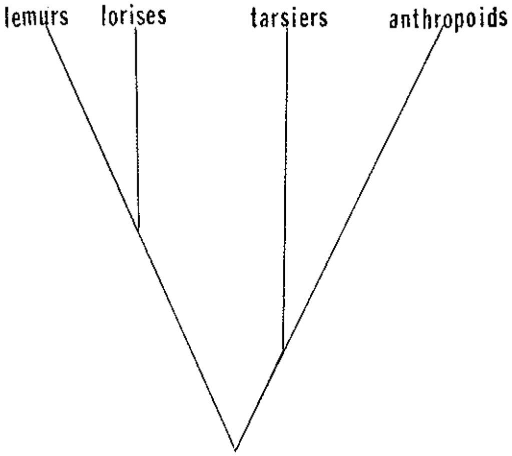

lemurs
lorises
tarsiers
anthropoids

FIG. 6

tulate incisors (these would have to evolve into the tooth comb), C/P complex, sexual dimorphism (which further implies something about the anthropoid-like behaviors of adapids) and symphyseal fusion. Thus while many adapids were lemur-like the fossil evidence suggests that they are not directly related to lemurs and lorises. Instead, it is suggested in the panphenetic phylogeny that lemurs and lorises branched with the common ancestor of omomyids and adapids and represent a group of primates independently evolving in Africa and Asia from the Paleocene-Recent. In other words, this phylogeny predicts that another group of (probably) lemur-like primates (the true ancestors of lemurs and lorises) not descendants of adapids and showing none of their derived traits, existed in Africa from the Paleocene-Recent. This is the most important prediction of this panphenetic phylogeny and it should be the first one tested by new stratophenetic evidence.

Expansion of the field

Thus far I have discussed some of the current paleontological issues in human origins — those concerning the adaptations, phylogeny and taxonomy of past populations of organisms in or near our ancestry. From an anthropological perspective it is hoped that research into human origins would also contribute something to our knowledge about the nature of living humans. It is this dimension of the study of human origins which can be greatly expanded.

The central point of my comment is that human phylogeny did not begin 5-15 million years ago and that the present human system, the form and behavior of individuals and societies is the result of over 3 billion years of evolutionary events. As Bateson [35] suggests, there is something relevant in every step of phylogeny and among the steps. Those who study human origins and who are interested in contributing to a scientific statement about the nature of living men should begin with a knowledge of physics, chemistry and the events of biogenesis. Any evolutionary events since biogenesis which contributed to the present human condition are also relevant. Thus, what has been suggested is basically a diachronic expansion of the field.

In the process of expansion it will be necessary to recognize and help define the limitations of an evolutionary perspective when it is applied to *living* humans. The evolutionary process is a stochastic process. From a wide range of variation in gene pools, the result of the random events of independent assortment, crossing over and mutation, only some of the genetic possibilites will persist across generational time. Those that do are called adaptive and we think of them as having enhanced reproduction in some way. Adaptations are the result of multigenerational events and a nonrandom process which selects from a large number of more or less randomly occurring possibilities. But for those interested in living men there is also another stochastic process occurring. It is intragenerational and it concerns individuals, not immense crowds or classes of individuals. I refer to a set of phenomena which collectively could be called homeostatic and descriptions of these phenomena are of a different logical type than descriptions of evolutionary phenomena.

Homeostatis can be defined in a number of ways. A physicist might define it for living matter as the point of maximum negentropy. A behaviorist might use a definition which states that it is the satisfaction of needs and drives or a reduction of tensions in tissues. Homeostatic responses may or may not be adaptive — the selective process is drive reduction related.

Perhaps the most important homeostatic mechanism in humans is learning. More so than in any other animal, learning and learned behaviors in man play a greater rôle in the satisfaction of needs and drives. To quote Bateson [35] "We face then, two great stochastic systems that are partly in interaction and partly isolated from each other. One system is within the individual and is called *learning*; the other is immanent in heredity and in populations and is called *evolution*. One is a matter of a single lifetime; the other is a matter of multiple generations of many individuals". Where the two stochastic systems meet is in the fact that the limits and potentials of what can be achieved by homeostatic mechanisms are fixed by genetics. In order to be more complete, scientific statements about living men must come to grips with both stochastic systems.

REFERENCES

[1] SIMONS E. L., « Sci. Amer. », *236*, 28-35 (1977).

[2] WASHBURN S. L., « Cold Spring Harbor Symposia on Quantitative Biology », *15*, 67-78 (1950).

[3] WASHBURN S. L., *Classification and Human Evolution*, Aldine, Chicago, pp. 190-203 (1963).

[4] WASHBURN S. L., « Sci. Amer. », *239*, 194-208 (1978).

[5] GREENFIELD L. O., in press *New Interpretations of Ape and Human Ancestry*. Plenum, New York.

[6] FRAYER D. W., « Yrbk. Phys. Anthrop. », *18*, 19-30 (1976).

[7] GREENFIELD L. O., Ph. D. Thesis, University of Michigan (1977).

[8] GREENFIELD L. O., « J. Hum. Evol. », *7*, 345-359 (1978).

[9] GREENFIELD L. O., « Amer. J. Phys. Anthrop. », *50*, 527-548 (1979).

[10] GREENFIELD L. O., « Amer. J. Phys. Anthrop. », *52*, 351-365 (1980).

[11] PILBEAM D. R. *et al.*, « Nature », *270*, 689-695 (1977).

[12] MOLNAR S. and GANTT D. G., « Amer. J. Phys. Anthrop. », *46*, 447-454 (1977).

[13] KAY R. F., « Amer. J. Phys. Anthrop. », *55*, 141-151 (1981).

[14] GREGORY W. K. and HELLMAN M., « Anthrop. Pap. Amer. Mus. Nat. Hist. », *28*, 1-123 (1926).

[15] ANDREWS P. and TEKKAYA I., « Paleontology », *23*, 85-95 (1980).

[16] PILBEAM D. R., « Nature » (198?).

[17] SMITH R. J. and PILBEAM D. R., « Nature », *284*, 447-448 (1980).

[18] SIMONS E. L., « J. Hum. Evol. », *5*, 511-528 (1976).

[19] GOODMAN M., *Phylogeny of the Primates*. Plenum Press, New York, pp. 219-248 (1975).

[20] GOODMAN M., *Molecular Evolution*. Sinauer, Sunderland, Mass., pp. 141-159 (1976).

[21] SARICH V. M. and WILSON A. C., « Science », *158*, 1200 (1967).

[22] WILSON A. C. and SARICH V. M., « Proc. Nat. Acad. Sci. », *63*, 1088-1093 (1969).

[23] SARICH V. M., *Perspectives on Human Evolution*, Holt, Rinehart, and Winston, New York, pp. 94-121 (1968).

[24] RADINSKY L., « Science », *200*, 1182-1183 (1978).

[25] KAY R. F., « Amer. J. Phys. Anthrop. », *43*, 195-216 (1975).

[26] HYLANDER W. L., « Science », *189*, 1095-1098 (1975).

[27] WOLPOFF M. H., in press *Current Anthrop.*

[28] JOHANSON D. C. and WHITE T. D., « Science », *203*, 321-330 (1979).

[29] JOHANSON D. C. *et al.*, « Kirtlandia », *28*, 1-14 (1978).

[30] WHITE T. D., « Amer. J. Phys. Anthrop. », *46*, 197-230 (1977).

[31] ANDREWS P. and TOBIEN H., « Nature », *268*, 699-701 (1977).

[32] SIMPSON G. G., *Phylogeny of the Primates*. Plenum Press, New York and London, pp. 3-19 (1975).

[33] SZALAY F. S., « Bull Amer. Mus. Nat. Hist. », *156*, 157-450 (1976).

[34] GINGERICH P. D., « J. Hum. Evol. », *10*, 345-374 (1981).

[35] BATESON G., *Mind and Nature*. Bantam Books, New York (1979).

HOMINOID EVOLUTION AND HOMINID ORIGINS

DAVID PILBEAM
Department of Anthropology Peabody Museum, Harvard University
Cambridge, U.S.A.

Introduction

This essay on hominoid evolution attempts to integrate recent advances from a number of disparate fields. I will concentrate on the fossil record, my primary area of interest (perhaps expertise as well) but I will also discuss other work, including functional-anatomical studies of primates and molecular genetics. There has been considerable progress in all areas, so much so that positions need rethinking regularly. Enough new information is available now to permit what I believe to be a reasonable synthesis of neontological and paleontological data on hominoids. Although the fossil record of very early hominids and their precursors is, to put it mildly, poor, a broader look at hominoid evolution can, I think, tell us something about hominid origins.

As with earlier reviews (Pilbeam, 1980), I have chosen the essay style, for several reasons. There are already a number of other recent comprehensive and technical reviews of the hominoid fossil record (Simons, 1981; Greenfield, 1979, 1980; Kay, 1982b; Pilbeam, 1979), and I prefer to discuss more "synthetic" issues within a less formal framework. I would also like to reach as wide an audience as possible.

A phylogeny that can combine plausibly fossil, comparative anatomical, and molecular data is likely to be more acceptable than one based on a single body of evidence. I am less sanguine than I used to be about the extent to which fossils can inform us about the sequence and timing of branching in hominoid evolution. The fossil record is still, of course, the only evidence for unique ancestral states; it remains to be seen how successfully such states can be interpreted in past species, given that those species are different from their putative living descendants.

The view that a species of *Ramapithecus* is an early hominid, ancestral to *Australopithecus* and *Homo* and not to any apes, is probably now a minority view among paleoanthropologists. In the 1960's, the fragmentary jaws and isolated teeth of *Ramapithecus* could plausibly be interpreted as early hominids (Simons, 1961; Pilbeam, 1966) given prevailing assumptions about the nature and course of hominoid evolution (Pilbeam, 1980; Wolpoff, 1982). This meant that certain characters seen in both *Ramapithecus* and *Australopithecus*, such as robust mandibles and thick molar enamel caps, were viewed as shared derived features. This view was challenged by other paleontologists (for example, Robinson, 1972; Frayer, 1974; Greenfield, 1980; Andrews, 1982) but has been upheld recently by Kay and Simons (1982), Kay (1982b), and Simons (1981).

Another and in the long run more serious challenge to the status of *Ramapithecus* came from work on the molecular record. Early analyses by Goodman comparing the immunospecificity of various serum proteins (Goodman, 1963) showed that the hominoids could be divided genetically into two groups that probably reflected branching patterns: an "Asian" grouping of *Pongo* and *Hylobates* and an "African" one comprising *Pan*, *Gorilla*, and *Homo*. Such patterns were abundantly confirmed by later workers, most notably Sarich and Wilson (Sarich and Wilson, 1967; Wilson and Sarich, 1969). Using immunological techniques to compare primate albumins, they showed the close similarity of humans to the African apes, a similarity that was confirmed as more proteins were examined both immunologically and by sequencing (see papers in Goodman and Tashian, 1975), and as DNA was analyzed by various techniques: hybridization, restriction endonuclease mapping, and sequencing (Wilson, Carlson and White, 1977; Kohne, 1970; Benveniste and Todaro, 1976; Ferris, Wilson and Brown, 1981; Brown, Prager, Wang and Wilson, 1982; Sibley and Ahlquist, pers. comm.).

The close similarity of humans to African apes and the more distant relationships of the Asian apes is one of the most significant discoveries of the past century. We must now seek two, not one, common ancestors for apes and humans; further, this illustrates the extent to which molecular and organismal changes are "uncoupled" (King and Wilson, 1975), with profound consequences for unravelling the fossil record.

Sarich and Wilson and their coworkers noted a pattern of uniformity in their immunological data that they interpreted as being due to a regular rate of molecular evolution. Calibrating their molecular clock initially with an estimated divergence date of 30 million years for the human-Old World Monkey common ancestor, and later with 70 million years for the earliest primates (Sarich and Cronin, 1975), they estimated hominoid divergence dates considerably younger than those then advocated by most paleoanthropologists: 8 to 10 million years for Asian apes, 4 or 5 million years for the last common ancestor of hominids and African apes, reflecting the relative degrees of genetic distance from humans of orangs and gibbons, and of chimps and gorillas.

Recently some paleontologists have tried to reconcile molecular and fossil data (Greenfield, 1980; Andrews, 1982; Andrews and Cronin, in preparation; Pilbeam, 1979, 1980; Lipson and Pilbeam, 1982; Landau, Pilbeam and Richard, 1982).

I have had doubts about the hominid status of *Ramapithecus* since at least the mid 1970's, although I have avoided stating explicitly that it was *not* a hominid until I had a clearer idea of what it was! I now have that clearer view, almost entirely due to the discovery in Pakistan in 1980 of Middle and Late Miocene facial specimens of the hominoid *Sivapithecus indicus* (Pilbeam, 1982). The subsequent analyses of these fossils, preserving parts previously not well known, have triggered a series of insights that have crystallised new ideas for me.

I now think it unlikely that *Ramapithecus* is a hominid; nor is the similar genus *Sivapithecus* with which it is now often synonymised (Greenfield, 1980; Kay, 1982b; Kay and Simons, 1982; Andrews, 1982); I still prefer to maintain it as a separate genus, pending the discovery of more complete material. I also believe it likely that both these genera, and others, are specifically related to orangutans rather than to other hominoids, and imply a divergence date for orangs approximately twice that estimated by Sarich and Cronin (1975) and 60% greater than Andrews and Cronin's estimate (Andrews, 1982; Andrews and Cronin, in preparation).

I must emphasize that the relevant Miocene hominoid fossil record is still poor and fragmentary. However, it is expanding at a healthy rate, so we can certainly expect significant increases in information, and probably further major changes in our ideas. As this debate has flowed back and forth, as my views have changed, even as new fossils are added along with new information about geological age and paleoecology, I have become convinced that fossils by themselves can solve only parts of the puzzle, albeit important ones. And other parts of the puzzle may remain unresolved.

The contribution of the fossil record

At this point I would like to digress a little to talk about the nature of the hominoid fossil record, to discuss some of the problems we face. Many points are specific illustrations of more general paleontological problems.

First, the hominoid record is often poor. Large samples have been recovered from the early Miocene, but only of East Africa. One species, *Proconsul africanus*, is now known from a relatively complete skeleton (Andrews, 1978; Bosler, 1981; Walker and Pickford, 1982). It is probably as well sampled as *Australopithecus afarensis*, (see April 1982 issue of American Journal of Physical Anthropology) assuming that is only one species. Other early Miocene species are less well known, and there are sorting problems involved in dealing with unassociated material (Bosler, 1981).

Middle and Late Miocene hominoids are poorly known. The best sampled time is from around 10 to 7 million years ago, a period half as long as the combined Pliocene and Pleistocene, and the best sampled geographical area is Eurasia. Seven main localities or locality clusters stand out. The Vallès Penedes in Spain (Crusafont-Pairó and Hürzeler, 1969; Crusafont-Pairó and Golpe-Posse, 1973). Vathylakkos near Salonika in Greece (de Bonis and Melentis, 1977, 1978), Rudabanya in Hungary (Kretzoi, 1975), Yassorien in Turkey (Andrews and Tekkaya, 1980), the Potwar Plateau of Pakistan (Pilbeam, Meyer, Badgley, Rose, Pickford, Behrensmeyer and Shah, 1977; Pilbeam, Rose, Badgley and Lipschutz, 1980; Pilbeam and Smith, 1981; Pilbeam, 1982) Haritalyangar in India (Prasad, 1977), and Lufeng in China (Xu and Lu, 1979; Lu, Xu and Zhang, 1981; Wu, Han, Xu, Lu, Pan, Zhang and Xiao, 1981; Zhang, Zhou, Hu and Lin, 1981).

Of these the best samples judged by abundance and diversity of hominoids, and geochronological and contextual information, would be those from Pakistan, China and Greece. The best known species is probably *Sivapithecus indicus*, through material recovered in Pakistan (Pilbeam and Smith, 1981; Pilbeam, 1982; Pilbeam, Rose, Badgley and Lipschutz, 1980). Postcranial material of *S. indicus* is only tentatively attributed, since there are no associated remains for *any* Middle or Late Miocene hominoids. Even assuming that postcranial specimens can be correctly assigned, *S. indicus*, the best known later Miocene species, would still be hardly as well sampled as *Paranthropus robustus* from Kromdraai, or *Homo habilis* from Tanzania, Kenya and Ethiopia (Howell, 1978).

We shall need much better sampling of that three million year segment of Late Miocene time before we have information equivalent to what is known for similar time segments for South and East African Plio-Pleistocene hominids, and of course other equivalent time segments will eventually have to be similarly sampled.

Most Miocene hominoids are known from jaws and teeth. These body parts are difficult to classify, even when they are relatively complete. Equivalent parts in most living mammals provide poor criteria for sorting into species. This means that we probably underestimate past diversity. Further, these same body parts are subject to parallel evolution in living mammals. For example, cranial robusticity and thick molar enamel have evolved in several primate groups (Kinsey, 1974; Kay, 1981). Without careful analysis, what on closer examination are more likely parallelisms might be interpreted as shared derived or shared retained primitive characters. Morphoclinical polarities are thus hard to determine, making it difficult to link fossil species together, or fossil with living species (Cartmill, 1981).

The Miocene hominoids are, collectively, different from living species. They are also, probably, more diverse at any given time (certainly through time). Living hominoid species, and earlier hominids such as *Australopithecus* species, all appear specialised relative to earlier forms and are different from each other. All of these factors contribute to making the assessment of ancestor-descendant relationships in hominoids particularly difficult.

Finally, a major confounding problem with the study of hominoid evolution has been a set of pervasive assumptions that have rarely been made explicit (Landau, Pilbeam and Richard, 1982). First, that the apes are closely related and that hominids are divergent, different from all apes. Second, that in virtually all attributes hominids exhibit derived, apes primitive, character states. Third, that apes have changed little since the common ancestor(s). Molecular studies suggest strongly that the first statement is false; the others probably are too. A fourth problem has been the assumptions that fossils contribute information to treebuilding. It is my conviction that for much of the study of hominoid evolution, and this goes for some aspects of Pliocene and Pleistocene hominid evolution too, the fossils in fact are interpreted in terms of pre-existing frameworks. These tend to be "robust", often changing little through time despite the addition of new fossils (see, for example, the range of supposedly different tres in Johanson and White, 1979). Many were fossil-free, even fossil-proof (Pilbeam, 1981).

Times change. Perhaps we can now begin to put together syntheses that use a fossil record that is relatively undistorted by presentist interpretive frameworks.

The establishment of an evolutionary framework

How should we proceed to paint the complex picture of hominoid evolution? To start we need a framework, and it is to the genetic record, particularly at the molecular level, that we must first turn. It seems plausible that direct or close indirect measurements of genotypic structure are likely to reflect cladistic patterns. A wide variety of studies ranging from DNA hybridisation (Kohne, 1970; Benveniste and Todaro, 1976; Sibley and Ahlquist, pers. comm.), sequencing (Brown, Prager, Wang and Wilson, 1982), restriction endonuclease mapping (Ferris, Wilson and Brown, 1981), protein sequencing (for example, Romero-Herrera, Lieska, Goodman and Simons, 1979), immunology (Sarich and Cronin, 1975), and karyology (Dutrillaux, 1975; Miller, 1977; Yunis and Prakash, 1982) almost all suggest very strongly that the branching order for hominoid lineages from oldest to youngest runs gibbon, orang, then gorilla or chimp or human. The branching order for "African" hominoids is unclear, patterns being ambiguous from the chromosome, mitochondrial DNA, and DNA hybridisation evidence.

There is less agreement about molecular clocks. Since King and Jukes (1969) and Kimura (1968) first proposed plausible mechanisms to account for clock-like phenomena there have been arguments con and pro (Richmond, 1970; Uzzell and Corbin, 1971, 1972; Corbin and Uzzell, 1970; Uzzell and Pilbeam, 1971; Sarich and Cronin, 1975; Van Valen, 1974; Corruccini, Baba, Goodman, Ciochon and Cronin, 1980; Friday, 1981). There is still no consensus, although there is I think a majority view. This is that single proteins, or more specifically the exons that code for single proteins, are unlikely to evolve at exactly regular rates. This is now hardly surprising given the emerging complexity of the genome, organised turmoil if not chaos (Schopf, 1981), and the range of different mechanisms that promote genetic change.

Analyses of immunological data (Farris, 1972, 1981; Swofford, 1981) using tree-building techniques (Wagner trees) that do not assume regularity of evolutionary rates, suggest that clocks based on single genes probably do not keep accurate time. Over long time periods (40 million years) rates may vary on average no more than 25%, but over short or more recent time periods fluctuations may be much higher. Protein or DNA sequencing will not change this picture.

This has led some to argue that a better "clock" will be found by looking at the entire genome (10^9 base pairs or more compared to 10^3 for an average protein) by DNA hybridisation (Sibley and Ahlquist, 1981). By averaging rates of many genotypic segments which vary in mean rates and which fluctuate in rates, through the Central Limit Theory and Law of Large Numbers (Sibley and Adlquist, 1981), the average rate of change of the entire genome is expected to be uniform and therefore regular relative to time. If this inference is correct, then DNA hybridisation, coupled with appropriate fossil-based calibration points, should give the best estimates for branching times. This proposition, as all other similar proposals, needs thorough testing in groups such as rodents, bovids, and carnivores which have (unlike primates) an adequate fossil record for independent estimates of divergence dates (see Brownell, 1980; Jacobs and Pilbeam, 1980).

Recent results by Sibley and Ahlquist on hominoids which, although unpublished, they have generously permitted me to cite, are as follows. The "delta mode" values are direct reflections of percentage of base-pair mismatches in DNA hybrids and will also be proportional to divergence times. Relative to labelled human DNA (and labelled reciprocals give for the most part quite similar values (Sibley and Ahlquist, pers. comm.; Benveniste and Todaro, 1976)) the delta mode values are as follows: human-chimp (2.3), human-gorilla (3.3), human-orang (5.2), human-gibbon (5.8), human-cercopithecoids (7.3), human-ceboids (15.2). Salient inferences from these data would be that the Asian ape lineages diverged close together, indeed closer than the three "African" hominoids; and that humans are most closely related among living hominoids to chimpanzees.

Were *Ramapithecus* (and/or *Sivapithecus*) a hominid, and if the hybridisation data reflect accurately branching times, then a 14 to 16 million year human-chimp divergence would imply a human-orang split at 32 to 36 million years. For a variety of reasons this seems unlikely. Placing the human-chimp split at around or a little over 4 million years, the probable age of the oldest undoubted hominid material from Hadar in Ethiopia (Johanson, Taieb and Coppens, 1982), would give a human-cercopithecoid divergence of 13 million years, which again is unlikely.

Fitting fossils to frameworks

Given the molecular based framework, how should we proceed? We need to be able to assign fossils to particular lineages, or to relate their lineages to those of the framework; to hang the fossils on the framework, like hats on a rack. This can be done if characters can be recognised in particular living hominoids that are plausibly interpreted as derived relative to other living hominoids and to ancestors, and if those characters can be recognised in extinct species. Then the existence of inferred shared derived characters can be used to link past and present species. Clearly, statements about such characters can only be more or less probable, varying in degrees of inductive strength (Cartmill, 1981).

Using this approach, paleoanthropologists have linked australopithecines and other early hominids with *Homo sapiens* in Hominidae, because of the presence of plausibly inferred shared derived characters of skull, dentition, and postcranium. The ability to "tease out" such characters, a subject of much discussion, is a function of at least the following factors: an understanding of particular systems in living species (such as a tooth, the masticatory system, particular joints, joint complexes) and a reasonable fossil record (permitting the potential tracing of systems through time). Only then can plausible hypotheses be framed about the relevant state variables need to characterise such dynamic systems (Luenberger, 1979).

The African apes lack entirely a fossil record, making it extremely difficult to know what to expect of early apes and of ancestors shared with hominids. The Asian fossil record has expanded and clarified recently and may tell us something about Asian ape evolution, especially that of *Pongo.*

Since 1973 I have been codirector with Dr. S. M. Ibrahim Shah of the Geological Survey of Pakistan of a research project on hominoid evolution which has involved a program of field research in Pakistan. We work in Neogene sediments of Siwalik Group rocks exposed in the Potwar Plateau, ranging in age from 15 or 16 million years to under 4 million years. We have recovered many fossils and completed a great deal of geological and paleoecological work (Pilbeam, Behrensmeyer, Barry and Shah, 1979). From levels around 8 million years old we have a number of interesting new hominoids (Pilbeam, Rose, Badgley and Lipschutz, 1980; Pilbeam and Smith, 1981; Pilbeam, 1982), as well as a few younger and older specimens (13 to 7 million years). We have many new jaws and teeth, postcranial elements, and several important more complete specimens. A partial face from around 8 million and a palate that is 12 to 13 million years old, as yet unpublished, have been particularly thought-provoking.

My comments on these specimens are preliminary and lean heavily on the work of my colleague Dr. Steven Ward (Ward and Pilbeam, 1982). The new material is assigned to *Sivapithecus indicus*, and greatly expands our knowledge of it. Overall, *S. indicus* differs from all living hominoids, morphologically and, perhaps, ecologically. Postcranially it was a generalised chimp-sized ape, capable of arboreal climbing and hanging (Rose, 1982a, 1982b). Clearly not a biped, it may have included a greater bipedal component in its positional repertoire than do living pondigs. It had thick-enamelled teeth and robust mandibles, and shows tooth wear characterictic of living "frugivorous" primates such as *Pongo* and *Pan* (Walker, pers. comm.).

However, in a few features *S. indicus* resembles the orang closely (premaxilla, temporomandibular joint, orbital region), and these we interpret (Ward and Pilbeam, 1982) as being derived characters shared by *Sivapithecus* and *Pongo.* This means that we regard it as likely that the two are more closely related than either is to the other extant hominoids, to *Australopithecus*, or to *Proconsul*, and that *Sivapithecus* is not ancestral to *Australopithecus*, *Pan*, and *Gorilla.* Out best material of *S. indicus* is around 8 million years old (Pilbeam, 1982); an undescribed palate (Raza, pers. comm.; Raza, Pilbeam and Ward, in prep.) 12 to 13 million years old preserves some of these critical features. This puts a minimum age on the separation of *Pongo* from other living hominoids based on these attributes. If other possibly related Asian and African specimens are included, and if we also consider evidence of faunal shifts and paleogeographic changes, that separation can plausibly be pushed back to around 16 million years. This is based on material from Buluk (Harris and Watkins, 1974; Pickford, 1981; Walker, pers. comm. Ward, pers. comm.), from Saudi Arabia (Thomas, pers. comm.; Thomas, Sen, Khan, Battail and Ligabue, 1982; Hamilton, Whybrow and McClure, 1978; Andrews, Hamilton and Whybrow, 1978), and from Sind in Pakistan (Raza and Barry, in prep.).

I emphasize that the inferences about the "shared derived" nature of these similarities in *Sivapithecus* and *Pongo* are just that. They are hypotheses that will be strengthened or weakened as the fossil record expands with more relatively complete specimens, and as we know more of the genetics, developmental biology, and functional biology of these characters.

Some other later Miocene specimens show some of these features. It seems likely that the *Sivapithecus* face from Yassioren in Turkey (Andrews and Tekkaya, 1981) has similar premaxillary morphology. Ward (pers. comm.) thinks it likely that the premaxilla in the intriguing Greek Late Miocene hominoid *Ouranopithecus macedoniensis* also exhibits this feature (de Bonis and Melentis, 1977, 1978). Mandibules and dentitions of this form show marked dimorphism, assuming large and small canined morphs to be females and males. Kay (1982a) has argued that too much variability is present in this sample for it to be interpreted as one species. I think it is more likely that one species is sampled, perhaps with greater tooth size difference than in any living hominoid. Cheek tooth morphology of *Ouranopithecus* is more similar to that of early *Australopithecus* than are those of other Miocene hominoids (de Bonis, Johanson, Melentis and White, 1981). The significance of this is unclear.

Ramapithecus species, whether or not synonymised with *Sivapithecus*, have been described from sites that are widely distributed in time and space. In some cases, for example Fort Ternan in Kenya (Leakey, 1962; Walker and Andrews, 1973; Greenfield, 1979, 1980), "*Ramapithecus*" specimens may be females of a large-canined "*Sivapithecus*". If size dimorphism was very high in later Miocene hominoids, small and large morphs previously placed in separate species or genera may prove to be females and males. This is also a possibility (and I emphasize possibility only) at Rudabanya in Hungary (Kretzoi, 1975), where *Rudapithecus hungaricus* and *Bodvapithecus altipalatus* have been described, and at Lufeng in China (Xu and Lu, 1979), where *Ramapithecus lufengensis* and *Sivapithecus yunnanensis* have been named. The Lufeng sample is of very great importance in understanding hominoid evolution. It is from a single small locality representing a short time period around 8 million years ago; abundant plant and animal remains are known; and over 400 isolated hominoid teeth, a dozen or more jaws, and several complete though very distorted skulls have been recovered. Dentally, the material shows resemblances both to *Sivapithecus-Ramapithecus* in Pakistan and to *Pongo*. Premaxillary morphology may resemble them too (Badgley, pers. comm.).

The status of the type material of *Ramapithecus* is unclear. New specimens from Pakistan, especially anterior teeth and mandibles, exhibit a heterogeneity unlikely to represent one species (*contra* de Bonis, 1981). There are differences between *Ramapithecus* and *Sivapithecus* in maxillary, mandibular, and dental morphology, although the former taxon is the less well known of the two. There is little evidence for very reduced canine dimorphism (contra Kay, 1982a) in these samples. For the moment I prefer to be conservative and retain *Ramapithecus* for some of the Pakistani and Indian hominoids. Such a view could easily change with the discovery of material as complete as the newer *Sivapithecus* facial specimens. The type of *R. brevitrostris* (YPM 13799) from Haritalyangar in India has a premaxillary region that probably resembled that of *Sivapithecus* (Ward and Pilbeam, 1982; Lipson and Pilbeam, 1982).

Summarising the Eurasian evidence, specimens of *Sivapithecus, Ramapithecus* and possibly *Ouranopithecus* and "*Sivapithecus*"-"*Ramapithecus*" from Lufeng exhibit a few features that can be interpreted as derived characters shared with *Pongo*. If correct, this places all of them outside Hominidae, and puts the human-orang divergence back to at least 13 million years and likely to 16 million years. Given this calibration point, the following approximate divergence times can be estimated for Anthropoidea, using the DNA hybridisation delta mode values cited earlier: human-chimp (7 million years); human-gorilla (10 million); human-gibbon (18 million years); human-cercopithecoid (23 million); human-ceboid (47 million).

Overview of hominoid evolution

I shall now summarise briefly by discussing a few significant steps in hominoid evolution.

The first species recognisably similar to living hominoids are those from the Early Miocene of Kenya and Uganda, 22 to 17 million years old. Recent finds of *Proconsul africanus* and *P. nyanzae* (Walker and Pickford, 1982) have greatly expanded our knowledge of their postcrania. They are uniquely different from living catarrhines, but show some significant similarities to living hominoids. They were probably generalised arboreal species, likely below-branch feeders (Rose, 1982a; Aiello, 1981), and probably postdate the branch point leading to cercopithecoids. Early cercopithecoids are present at Napak (Pilbeam and Walker, 1968), Buluk (Pickford, 1981), Maboko (Andrews, Meyer, Pilbeam, Van Couvering and Van Couvering, 1981), and in North Africa (Delson, 1979), and document a split older than 18 to 20 million years (DNA estimate, 23 million). One or more of the smaller hominoids from these early Miocene deposits

(Harrison, 1981; Fleagle, 1975) could be close to the ancestry of hylobatids (DNA estimate, 18 million years).

The earliest evidence for "*Sivapithecus*"-like morphologies comes from Buluk (Pickford, 1981; Walker, pers. comm.; Ward, pers. comm.; pers. obs.), and Maboko (Andrews, Meyer, Pilbeam, Van Couvering and Van Couvering, 1981), both estimated at 15 to 17 million years, although if the type of *S. africanus* is indeed from Rusinga an older age might obtain (Andrews and Molleson, 1979). I have tentatively selected 16 million years as the best conservative estimate for the first appearance of non-*Proconsul* type hominoids. Their first appearance in South Asia is documented in Sind in Pakistan at about this time (Raza and Barry, in prep.). Faunal and geological evidence (Van Couvering, 1972) indicates closure of the eastern Tethys at about this time. I suggest that the closeness of human-orang and human-gibbon divergence estimates may reflect this paleogeographical event.

Following their spread into Asia, we know little of the fate of hylobatids (Li, 1978). Large hominoids evidently diversified, represented by species discussed above as the genera *Sivapithecus, Ramapithecus*, and *Auranopithecus*. They are characterised by a few cranial-facial features seen later in orangs, by sometimes markedly dimorphic dentitions, with thick enamelled cheek teeth, and, where preserved, by generalised skeletons. Habitats likely ranged from forest to woodland (Andrews, 1981). *Pongo* is possibly the living, greatly changed and specialised descendant of one of these later Miocene Eurasian hominoids (Smith and Pilbeam, 1980, 1981; Pilbeam, 1982; Lipson and Pilbeam, 1982; Ward and Pilbeam, 1982; Andrews, 1982).

For Africa we have few relevant remains. From Maboko and Fort Ternan there are a handful of "*Sivapithecus*"-"*Ramapithecus*" specimens (Andrews and Walker, 1976). The palate from Moroto in Uganda described as *Proconsul major* (Pilbeam, 1969) is probably not (Martin, 1981), a conclusion with which I now agree. It may be Middle Miocene in age (Pickford, 1981; Pickford and Tassy, 1980; Tassy, 1979). In premaxillary and palatal morphology (Ward and Pilbeam, 1982) it resembles earlier *Proconsul* specimens and is probably primitive. Cheek tooth enamel was, as in *P. nyanzae* and *P. africanus*, thicker than in living pongids.

A single upper molar from the Ngorora Formation of the Baringo sequence in Kenya, with an age estimate of 10 to 11 million years (Bishop and Chapman, 1970; Bishop and Pickford, 1975) has thick enamel. A lower molar from Lukeino in Baringo, between 6 and 7 million years old, also has thick enamel (Pickford, 1975). In their analysis of this specimen, McHenry and Corruccini (1980), underestimated crown height; the specimen is broken above the cervix so only a minimum height estimate is possible, so their conclusion that the specimen is chimp-like may need reconsidering. The Lothagam jaw (Patterson, Behrensmeyer and Sill, 1970) is between 3.7 million and 8.3 million years old, and may be around 6 million years old; it resembles *A. afarensis* (Ward, pers. comm.; Walker, pers. comm.). According to McHenry and Corruccini (1980) it is closer to chimp than is *A. afarensis*. However, since the Ngorora, Lukeino, and Lothagam specimens are all isolated teeth or fragmentary lower jaws, and since we are not in a position yet to infer the likely states of these characters in early *Pan*, early *Gorilla*, earliest hominids, or their immediate common ancestors, they contribute little to our understanding of African hominoid branching patterns. Lukeino and Lothagam are at least compatible with a human-chimp branching time of around 7 million years.

Material from Hadar and Laetoli, dated between a little over 4 million and a little under 3 million years, is clearly hominid (Johanson and White, 1979). The degree to which various characters are relatively primitive or relative specialised is unclear; it seems unlikely that these hominids are derived from species closely resembling *Gorilla* or *Pan* (Filler, 1980, 1981; Tuttle, 1981; Rose, 1982b). This implies that African apes may be derived in several significant characters: possibly in having small cheek teeth with thin enamel caps (Kay, 1981), and in being knuckle-walkers (Tuttle, 1967). However, until an adequate Middle and Late Miocene record (from at least 12 million to 5 million years) is recovered from both West and Central as well as East Africa such inferences rest on very weak evidence.

Conclusions

Poor though the earlier hominoid fossil record is, it is compatible with a DNA-based branching sequence. If *Sivapithecus* or a related form is ancestral to *Pongo* then the Asian ape has changed substantially since the Late Miocene. It is also likely that the ancestors of gorilla, chimp, and hominids differed from their descendants as well, although until the African later Miocene hominoid record is as well documented as the Asian one, that inference must be treated even more sceptically than the other.

However, it is distinctly possible that *all* living hominoids have changed since the Late Miocene.

Hominids are probably not derived in all features. Thus it is possible that many features of the dentition, face, and mandible of early *Australopithecus* are primitive and equivalent features in African apes derived. Similarly, some postcranial characters of early hominids may be retained primitive features; perhaps Miocene hominids were more frequently bipedal than the living pongids. If these guesses are correct, then we shall have to be very careful about assigning hominoid fossils between 6 and 12 million years old to particular lineages. The next twenty years should be very exciting ones for the study of hominid origins.

REFERENCES

AIELLO L. C., *Locomotion in the Miocene Hominoidea*, in « Aspects of human evolution », ed. C. Stringer, Taylor and Francis, pp. 63-97 (1981).

ANDREWS P., *A revision of the Miocene Hominoidea of East Africa*, « Bull. Brit. Mus. (Nat. Hist.) », *30*, 85-224 (1978).

ANDREWS P., *Hominoid habitats of the Miocene.* « Nature », *289*, 749 (1981).

ANDREWS P., *Hominoid evolution.* « Nature », *295*, 185-186 (1982).

ANDREWS P., HAMILTON W. R. and WHYBROW P. J., *Dryopithecines from the Miocene of Saudi Arabia.* « Nature », *274*, 249-251 (1978).

ANDREWS P., MEYER G. E., PILBEAM D. R., VAN COUVERING J. A. and VAN COUVERING J. A. H., *The Miocene fossil beds of Maboko Island, Kenya: geology, age, taphonomy and palaeontology.* « J. Hum. Evol. », *10*, 35-48 (1981).

ANDREWS P. and MOLLESON T. I., *The provenance of* Sivapithecus africanus. « Bull. Br. Mus. Nat. Hist. (Geol.) », *32*, 19-23 (1979).

ANDREWS P. and TEKKAYA I., *A revision of the Turkish Miocene hominoid* Sivapithecus meteai. « Palaeontol. », *23*, 85-95 (1980).

ANDREWS P. and WALKER A., *The primate and other fauna from Fort Ternan, Kenya*, in « Human Origins », eds. G. Isaac and E. McCown, Benjamin, pp. 279-306 (1976).

BENVENISTE R.E. and TODARO G.J., *Evolution of type C viral genes: evidence for an Asian origin of man.* « Nature », *261*, 101-108 (1976).

BISHOP W. W. and CHAPMAN G. R., *Early Pliocene sediments and fossils from the Northern Kenya Rift Valley.* « Nature », *226*, 914-918 (1970).

BISHOP W. W. and PICKFORD M. H. L., *Geology, fauna and palaeoenvironments of the Ngorora Formation, Kenya Rift Valley.* « Nature », *254*, 185-192 (1975).

DE BONIS L., *Les primates hominoides du Miocène et le problème du Ramapitheque.* « Coll. Int. CNRS », *599*, 49-53 (1981).

DE BONIS L., JOHANSON D., MELENTIS J. and WHITE T., *Variations métriques de la denture chez les Hominidés primitifs: comparaison entre* Australopithecus afarensis *et* Ouranopithecus macedoniensis. « C.R. Acad. Sc. Paris », *292*, 373-376 (1981).

DE BONIS L. and MELENTIS J., *Les primates hominoides du Vallésien de Macédoine* (Grèce). *Étude de la machoire inférieure.* « Geobios », *10*, 849-885 (1977).

DE BONIS L. and MELENTIS J., *Les Primates Hominoides du Miocène Supérieur de Macédoine.* « An. Paleontol. (Vert.) », *64*, 185-202 (1978).

BOSLER W., *Species groupings of Early Miocene dryopithecine teeth from East Africa.* « J. Hum. Evol. », *10*, 151-158 (1981).

BROWN W. M., PRAGER E. M., WANG A. and WILSON A. C., *Mitochondrial DNA sequences of primates: tempo and mode of evolution.* « Cell », in press (1982).

BROWNELL E., *A study of rodent evolution.* Ph. D. diss., Yale University (1980).

CARTMILL M., *Hypothesis testing and phylogenetic reconstruction.* « Son. aus Z. f. zool. Syst. Evol. », *19*, 73-96 (1981).

CORBIN K. W. and UZZELL T., *Natural selection and mutation rates in mammals.* « Amer. Nat. », *104*, 37-53 (1970).

CORRUCCINI R. S., BABA M., GOODMAN M., CIOCHON R. L. and CRONIN J. E., *Non-linear macromolecular evolution and the molecular clock*, « Evol. », *34*, 1216-1219 (1980).

CRUSAFONT-PAIRÓ M. and GOLPE-POSSE J.M., *New pongids from the Miocene of Vallès Penedes Basin (Catalonia, Spain).* « J. Hum. Evol. », *2*, 17-23 (1973).

CRUSAFONT-PAIRÓ M. and HURZELER J., *Catálogo comentado de los Póngidos fósiles de España.* « Acta Geol. Hisp. », *4*, 44-48 (1969).

DELSON E., Prohylobates (*Primates*) *from the Early Miocene of Libya: a new species and its implications for cercopithecid origins.* « Geobios. », *12*, 725-733 (1979).

DUTRILLAUX B., *Sur la nature et l'origine des chromosomes humains.* « Mon. Ann. Génét. », L'expansion Scientifique, Paris (1975).

FARRIS J.S., *Estimating phylogenetic trees from distance matrices.* « Amer. Nat. », *106*, 645-668 (1972).

FARRIS W.J., *Distance data in phylogenetic analysis,* in « Advances in cladistics », eds. V.A. Funk and D.R. Brooks, N. Y. Botanical Garden, pp. 3-23 (1981).

FERRIS S.D., WILSON A.C. and BROWN W.M., *Evolutinary tree for apes and humans based on cleavage maps of mitochondrial DNA.* « Proc. Natl. Acad. Sci. USA », *78*, 2432-2436 (1981).

FILLER A.G., *Anatomical evidence for the « hylobatian » model of hominid evolution.* « Am. J. Phys. Anthrop. », *52*, 226 (1980).

FILLER A.G., *Anatomical specialization in the hominoid lumbar region.* « Am. J. Phys. Anthrop. », *54*, 218 (1981).

FLEAGLE J.G., *A small gibbon-like hominoid from the Miocene of Uganda.* « Folia Primatol. », *24*, 1-15 (1975).

FRAYER D., *A reappraisal of* Ramapithecus. « Yrbk. Phys. Anthrop. », *18*, 19-30 (1974).

FRIDAY A.E., *Hominoid evolution: the nature of biochemical evidence,* in « Aspects of human evolution », ed. C. Stringer, Taylor and Francis, pp. 1-23 (1981).

GOODMAN M., *Serological analysis of the systematics of recent hominoids.* « Hum Biol. », *35*, 377-424 (1963).

GOODMAN M. and TASHIAN R.E. eds., *Molecular anthropology,* Plenum (1975).

GREENFIELD L., *On the adaptive pattern of* « Ramapithecus ». « Am. J. Phys. Anthrop. », *50*, 527-548 (1979).

GREENFIELD L., *A late divergence hypothesis.* « Am. J. Phys. Anthrop. », *52*, 351-365 (1980).

HAMILTON W.R., WHYBROW P.J. and MCCLURE H.A., *Fauna of fossil mammals from the Miocene of Saudi Arabia.* « Nature », *274*, 248-249 (1978).

HARRIS J.M. and WATKINS R., *New early Miocene vertebrate locality near Lake Rudolf, Kenya.* « Nature », *252*, 576-577 (1974).

HARRISON T., *New finds of small fossil apes from the Miocene locality at Koru in Kenya.* « J. Hum. Evol. », *10*, 129-137 (1981).

HOWELL F.C., *Hominidae,* in « Evolution of African Mammals », eds. V.J. Maglio and H.B.S. Cooke, Harvard University, pp. 154-248 (1978).

JACOBS L.L. and PILBEAM D., *Of mice and men: fossil-based divergence dates and molecular « clocks ».* « J. Hum. Evol. », *9*, 551-555 (1980).

JOHANSON D.C., TAIEB M. and COPPENS Y., *Pliocene hominids from the Hadar Formation, Ethiopia* (1973-1977): *Stratigraphic, chronologic, and paleoenvironmental contexts, with notes on hominid morphology and systematics.* « Am. J. Phys. Anthrop. », *57*, 373-402 (1982).

JOHANSON D.C. and WHITE T.D., *A systematic assessment of early African hominids.* « Science », *202*, 321-330 (1979).

KAY RICHARD, *The nut-crackers — a new theory of the adaptations of the Ramapithecinae.* « Am. J. Phys. Anthrop. », *55*, 141-151 (1981).

KAY R. F., *Sexual dimorphism in Ramapithecinae.* « Proc. Natl. Acad. Sci. USA », *79*, 209-212 (1982a).

KAY R., Sivapithecus simonsi, *a new species of Miocene hominoid, with comments on the phylogenetic status of the Ramapithecinae.* « Int. J. Primatol. », in press (1982b).

KAY R. and SIMONS E. L., *A reassessment of the relationship between late Miocene and subsequent Hominoidea,* in « New interpretations of ape and human ancestry », eds, R.L. Ciochon and R.F. Corruccini, Plenum, in press (1982).

KIMURA M., *Evolutionary rates at the molecular level.* « Nature », *217*, 624-626 (1968).

KING J.L. and JUKES T.M., *Non-Darwinian evolution.* « Science », *164*, 788-798 (1969).

KING M.-C. and WILSON A. C., *Evolution at two levels in humans and chimpanzees.* « Science », *188*, 107-116 (1975).

KINZEY W., *Ceboid models for the evolution of the hominoid dentition.* « J. Hum. Evol. », *3*, 193-203 (1974).

KOHNE D. E., *Evolution of higher-organism DNA.* « Quart. Rev. Biophys. », *3*, 327-375 (1970).

KRETZOI M., *New ramapithecines and* Pliopithecus *from the Lower Pliocene of Rudabanya in north-eastern Hungary.* « Nature », *257*, 578-581 (1975).

LANDAU M., PILBEAM D. and RICHARD A., *Human origins a century after Darwin.* « Bioscience », in press (1982).

LEAKEY L. S. B., *A new Lower Pliocene fossil primate from Kenya.* « Ann. Mag. Nat. Hist. », *13*, 689-696 (1962).

LI C-K., *A Miocene gibbon-like primate from Shihhung, Kiangsu Province.* « Vert. PalAsiat. », *16*, 187-192 (1978).

LIPSON S. and PILBEAM D., *Ramapithecus, La Recherche,* in press (1982).

LU QINGWQU, XU QINGUA and ZHENG LIANG, *Preliminary research on the cranium of* Sivapithecus yunnanensis. « Vert. PalAsiat. », *19*, 101-106 (1981).

LUENBERGER D. G., *Introduction to dynamic systems.* Wiley (1979).

MARTIN L., *New specimens of* Proconsul *from Koru, Kenya.* « J. Hum. Evol. », *10*, 139-150 (1981).

MCHENRY H. M. and CORRUCCINI R. S., *Late Tertiary hominoids and human origins.* « Nature », *285*, 397-398 (1980).

MILLER D. A., *Evolution of primate chromosomes.* « Science », *198*, 1116-1124 (1977).

PATTERSON B., BEHRENSMEYER A. K. and SILL W. D., *Geology and fauna of new Pliocene locality in North-western Kenya.* « Nature », *226*, 918-921 (1970).

PICKFORD M., *Late Miocene sediments and fossils from the Northern Kenya Rift Valley.* « Nature », *256*, 279-284 (1975).

PICKFORD M. and TASSY P., *A new species of* Zygolophodon *(Mammalia, Proboscidea) from the Miocene hominoid localities of Meswa Bridge and Moroto (East Africa).* « N. Jb. Geol. Palaont. Mh. », *H.4*, 235-251 (1980).

PICKFORD M., *Preliminary Miocene mammalian biostratigraphy for Western Kenya.* « J. Hum. Evol. », *10*, 73-98 (1981).

PILBEAM D., BEHRENSMEYER A. K., BARRY J. C. and SHAH S. M. I., *Miocene sediments and faunas of Pakistan.* « Peabody Mus. Postilla », *179* (1979).

PILBEAM D., MEYER G. E., BADGLEY C., ROSE M. D., PICKFORD M. H. L., BEHRENSMEYER A. K. and SHAH S. M. I., *New hominoid primates from the Siwaliks of Pakistan and their bearing on hominoid evolution.* « Nature », *270*, 689-695 (1977).

PILBEAM D., ROSE M. D., BADGLEY C. and LIPSCHUTZ B., *Miocene hominoids from Pakistan.* « Peabody Mus. Postilla », *181* (1980).

PILBEAM D. and SMITH R., *New skull remains of* Sivapithecus *from Pakistan.* « Mem. Geol. Surv. Pakistan », *11*, 1-13 (1981).

PILBEAM D., *Notes on* Ramapithecus, *the earliest known hominid, and* Dryopithecus. « Am. J. Physo. Anthrop. », *25*, 1-6 (1966).

PILBEAM D., *Tertiary Pongidae of East Africa: evolutionary relationships and taxonomy.* « Peabody Mus. Bull. », *31* (1969).

PILBEAM D., *Recent finds and interpretations of Miocene hominoids.* « Ann. Rev. Anthropol. », *8*, 333-352 (1979).

PILBEAM D., *Major trends in human evolution,* in « Current argument on early man », ed. L.-K. Konigsson, Pergamon, pp. 261-285 (1980).

PILBEAM D., *Foreword,* in « Missing links », John Reader, Little Brown, pp. 7-10 (1981).

PILBEAM D., *New hominoid skull material from the Miocene of Pakistan.* « Nature », *295*, 232-234 (1982).

PRASAD K. N., *Review of Miocene Anthropoidea from India and adjacent countries.* « J. Palaeont. Soc. India », *20*, 382-390 (1977).

RICHMOND R., *Non-Darwinian evolution: a critique.* « Nature », *225*, 1025-1028 (1970).

ROBINSON J. T., *Early hominid posture and locomotion,* University of Chicago (1972).

ROMERO-HERRERA A., LIESKA N., GOODMAN M. and SIMONS E. L., *The use of amino acid sequence analysis in assessing evolution.* « Biochimie », *61*, 767-779 (1979).

ROSE M. D., *Miocene hominoid postcranial morphology: monkey-like, ape-like, neither, or both?* in « New interpretations of ape and human ancestry », eds. R. L. Ciochon and R. F. Corruccini, Plenum, in press (1982a).

ROSE M. D., *Food acquisition and the evolution of positional behavior: the case of bipedalism,* in « Food acquisition and processing in Primates », eds. R. L. Ciochon and R. F. Corruccini, Plenum, in press (1982b).

SARICH V. M. and CRONIN J. E., *Molecular systematics of the primates,* in « Molecular anthropology », eds. M. Goodman and R. E. Tashian, Plenum, pp. 141-169 (1975).

SARICH V. M. and WILSON A. C., *Immunological time scale for hominid evolution.* « Science », *158*, 1200-1203 (1967).

SCHOPF T. J. M., *Evidence from findings of molecular biology with regard to the rapidity of genomic change: implications for species durations,* in « Paleobotany, paleoecology and evolution », vol. I, ed. K. J. Niklas, Praeger, pp. 135-192 (1981).

SIBLEY C. G. and AHLQUIST J. E., *The phylogeny and relationships of the ratite birds as indicated by DNA-DNA hybridization,* in « Evolution today, Proc. Second Int. Cong. System. Evol. Biol. », eds. G.G.E. Scudder and J.L. Reveal, 301-335 (1981).

SIMONS E. L., *The phyletic position of Ramapithecus.* « Peabody Mus. Postilla », *57* (1961).

SIMONS E. L., *Man's immediate forerunners.* « Phil. Trans. R. Soc. Lond. », *B. 292*, 21-41 (1981).

SMITH R. J. and PILBEAM D. R., *Evolution of the orang-utan.* « Nature », *284*, 447-448 (1980).

SWOFFORD D. L., *On the utility of the distance Wagner procedure,* in « Advances in cladistics », eds. V. A. Funk and D. R. Brooks, N. Y. Botanical Garden, pp. 25-43 (1981).

TASSY P., *Les Probiscidiens (Mammalia) du Miocene d'Afrique orientale: résultats préliminaires.* « Bull. Soc. geol., France », *21,* 265-269 (1979).

THOMAS H., SEN S., KHAN M., BATTAIL B. and LIGABUE G., *The Lower Miocene fauna of As Sarrar (Western Province, Saudi Arabia).* ATLAL, in press (1982).

TUTTLE R. H., *Knuckle-walking and the evolution of hominoid hands.* « Am. J. Phys. Anthrop. », *26,* 171-206 (1967).

TUTTLE R. H., *Evolution of hominid bipedalism, and prehensile capabilities.* « Phil. Trans. R. Soc. Lond. », *B, 292,* 89-94 (1981).

UZZELL T. and CORBIN K. W., *Fitting discrete probability distributions to evolutionary events.* « Science », *172,* 1089-1096 (1971).

UZZELL T. and CORBIN K. W., *Evolutionary rates in cistrons specifying mammalian hemoglobin α- and β-chains: phenetic versus patristic measurements.* « Amer. Nat. », *106,* 555-573 (1972).

UZZELL T. and PILBEAM D., *Phyletic divergence dates of hominoid primates: a comparison of fossil and molecular data.* « Evol. », *25,* 615-635 (1971).

VAN COUVERING J., *Radiometric calibration of the European Neogene,* in « Calibration of hominoid evolution », ed. W. W. Bishop, Scottish Academic Press, pp. 247-271 (1972).

VAN VALEN L., *Molecular evolution as predicted by natural selection.* « J. Mol. Evol. », *3,* 89-101 (1974).

WALKER A. and ANDREWS P., *Reconstruction of the dental arcades of Ramapithecus wickeri.* « Nature », *244,* 313-314 (1973).

WALKER A. C. and PICKFORD M., *New postcranial fossils of* Proconsul africanus *and* Proconsul nyanzae, in « New interpretations of ape and human ancestry », eds. R. L. Ciochon and R.F. Corruccini, Plenum, in press (1982).

WARD S. and PILBEAM D., *Maxillofacial morphology of Miocene hominoids from Africa and Indo-Pakistan,* in « New interpretations of ape and human ancestry », eds. R.L. Ciochon and R.F. Corruccini, Plenum, in press (1982).

WILSON A. C., CARLSON S. S. and WHITE T. J., *Biochemical evolution.* « Ann. Rev. Biochem. », *46,* 573-639 (1977).

WILSON A. C. and SARICH V. M., *A molecular time scale for human evolution.* « Proc. Natl. Acad. Sc. USA », *63,* 1088-1093 (1969).

WOLPOFF M., Ramapithecus *and hominid origins.* « Curr Anthrop. », in press (1982).

WU RUKANG, HAN DEFEN, XU QINGHUA, LU QINGWU, PAN YUERONG, ZHANG XINGYONG, ZHEN LIANG and XIAO MINGHUA, Ramapithecus *skull found first time in world.* « Vert. Pal. Asiat. », *26,* 1018-1021 (1981).

XU QINGHUA and LU QINGWU, *The mandibles of* Ramapithecus *and* Sivapithecus *from Lufeng, Yunnan.* « Vert. Pal. Asiat. », *17,* 1-13 (1979).

YUNIS J. J. and PRAKASH O., *The origin of man: a chromosomal pictorial legacy.* « Science », *215,* 1525-1530 (1982).

ZHANG XINGYONG, ZHOU GUOXING, HU YOUHENG and LIN YIPU, *Stratigraphy of* Ramapithecus*-bearing Pliocene of Lufeng, Yunnan.* « Mem. Beijing Nat. Hist. Mus. », *10,* 1-20 (1981).

L'ACQUISITION DE LA STATION ÉRIGÉE ET DE LA LOCOMOTION BIPÈDE CHEZ LES HOMINIDÉS

EDOUARD BONÉ
Labor. de Paléont. des Vertébrés et de Paléont. humaine,
Université Catholique de Louvain
Louvain-la-Neuve, Belgique

INTRODUCTION

On s'accorde généralement à citer quatre traits principaux distinguant la famille des Hominidés des autres Primates, notamment Pongidés: leur progressive expression au cours du Cénozoïque caractérise ce qu'on a coutume d'appeler le processus d'Hominisation. Il s'agit (1) de la spectaculaire expansion crânienne, (2) du développement parallèle d'une culture matérielle de plus en plus complexe, (3) de la réduction du massif dentaire antérieur et de la graduelle prépondérance des dents molaires, (4) du redressement postural enfin et de la locomotion bipède (Lovejoy, 1981).

Encore qu'elles doivent être de quelque manière en relation de fonctionnalité, ces diverses caractéristiques ne semblent pas être apparues de manière rigoureusement synchrone: tandis que l'expansion crânienne est relativement tardive ou n'a cessé du moins de s'exprimer jusque dans le Pleistocène supérieur, le redressement postural semble aujourd'hui beaucoup plus précoce, substantiellement réalisé il y a quelque 3 MA d'ici sans doute, voire davantage, chez des individus dont tout porte à croire qu'ils étaient dotés d'un cerveau encore fort réduit. L'apparition de l'outil — de l'outil de pierre du moins — a peut-être suivi d'un million d'années ou plus la conquête de la bipédie.

Les fouilles développées depuis un quart de siècle, du Transvaal aux Afars, dans l'Est-africain en particulier, ont beaucoup contribué à éclairer ces aspects du processus d'Hominisation, sans faire encore toutefois toute la lumière sur les circonstances, les étapes et les conditions du redressement postural. On voudrait ici faire le point sur ce problème particulier de l'acquisition de la station érigée et de la locomotion bipède chez les Hominidés.

Station érigée et locomotion bipède ont toujours été unanimement considérées comme caractéristiques de l'espèce *Homo sapiens*. Si on a pu émettre jadis des réserves sur les conditions et l'achèvement du processus de redressement dans certaines populations néandertaliennes, on a bien vite reconnu que l'acquisition de la verticalité par spécialisation locomotrice du train postérieur avait constitué un des éléments fondamentaux de l'hominisation. Très tôt après la découverte, à Trinil, en Indonésie, du fameux *Pithecanthropus* (1891) et en dépit des hésitations de Dubois lui-même, la science reconnaissait la verticalité bipède de celui qui allait devenir et demeurer précisément l'*Homo erectus*. Des questions subsistaient pourtant qui devaient se faire plus pressantes avec l'irruption sur la scène paléoanthropologique, de représentants plus anciens et plus primitifs de la famille des Hominidés, expressions plus frustes du processus hominisant: *Australopithecus*, *Homo habilis*, voire *Ramapithecus*. Ces questions n'ont pas toutes reçu une réponse adéquate encore.

Il pourrait suffire d'enregistrer le très éloquent témoignage de la bipédie proposé par les empreintes de pas laissées par *Australopithecus* sp. dans les tufs argileux de Laetolil, en Tanzanie, datés de ca. 3,5MA (Johanson et White, 1980). En réalité les traces découvertes à Laetolil n'ont sans doute pu être interprétées que sur la base des études développées depuis un demi-siècle à propos des spécialisations locomotrices des Hominidés du Pleistocène inférieur pour répondre aux questions suscitées par les premières découvertes du Transvaal.

Parmi les interrogations qui demeurent actuelles, il en est de plus urgentes: (1) sur le plan anatomo-fonctionnel d'abord: à quelle époque et par quel cheminement le redressement postural s'est-il imposé dans la famille des Hominidés? Peut-on, sur base des documents fossiles disponibles, en préciser les expressions ostéologiques? (2) Le redressement est-il vraiment spécifique du groupe en cours d'hominisation, ou peut-on reconnaître d'authentiques manifestations du même trend, fussent-elles moins parfaitement réalisées, parmi les primates non humains? (3) Quelles sont, pour les Hominidés, les implications comportementales du redressement et peut-on formuler des hypothèses fiables à propos des facteurs qui l'ont permis ou déterminé? Comment en particulier apprécier les schémas écologiques présentés à ce sujet?

On se limitera délibérément à l'examen des formes d'Hominidés antérieures à l'apparition d'*Homo erectus*, et à des groupes ancestraux ou latéraux de comparaison.

LA SYSTÉMATIQUE

Coppens (1979) a récemment proposé pour l'Afrique (de l'Est en particulier) une excellente organisation du matériel hominidé disponible au Pliocène terminal et Pleistocène inférieur, antérieurement au groupe *sapiens*. Selon ce schéma parfaitement satisfaisant, il est raisonnable de regrouper l'entièreté de la collection en deux genres *Australopithecus* et *Homo*, et cinq espèces: *A. afarensis*, *A. africanus*, *A. robustus/boisei*, *H. habilis* et *H. erectus*. (Pour la commodité, on réunit ici, sous une seule étiquette superspécifique *boisei*, les espèces allopatriques *robustus* et *boisei*, du Transvaal et du Rift respectivement).

La forme la plus ancienne du genre *Australopithecus*, *A. afarensis* (Johanson, White et Coppens, 1978), est actuellement repérée en Ethiopie dans la formation d'Hadar et dans les groupes A et B (formations d'Usno et de Shungura) de la basse vallée de l'Omo; au Kenya, dans la formation de Kubi Algi et à la base de la formation de Koobi Fora de l'Est Turkana; à Lothagam dans le SW Turkana, à Lukeino et Chemeron encore dans la région du Lac Baringo; en Tanzanie enfin, à Laetolil. Ces diverses formations s'échelonnent dans le temps de 6,5 MA (Lukeino) à 2,7 MA (Shungura, dans l'Omo).

L'espèce *A. africanus*, la forme gracile initialement décrite dans le Transvaal à Taung, Sterkfontein et Makapansgat, est actuellement reconnue aussi dans les groupes C-G de la vallée de l'Omo de l'Est Turkana et dans la gorge d'Olduvai (Lit I). En réalité le rajeunissement de la brèche de Taung (Tobias, 1973) jusqu'à 0,8 MA amène à revoir l'attribution spécifique du fossile type du genre *Australopithecus*, au demeurant jeune adolescent et dès lors malaisément interprétable. D'aucuns estiment qu'il pourrait être un représentant attardé de la forme *robustus*! S'il en était ainsi, les documents décidément *africanus* appartiendraient à une période étalée du Sud à l'Est africain de ca 3 MA à 1,6 MA.

La forme robuste, *A. boisei* (ancien *Paranthropus* ou *A. robustus* d'Afrique australe) est actuellement repérée du Transvaal (Swartkrans, Kromdraai et éventuellement Taung) au Grand Rift, et ici notamment dans les groupes C-K de l'Omo, en Etbiopie; dans les divers membres de la formation de Koobi Fora (Est Turkana) au autour du Lac Baringo, au Kenya; au Lac Natron (Peninj) et dans les lits I et II d'Olduvai (Tanzanie). Les documents les plus anciens remontent ainsi à 2,6 MA, les plus récents sont datés de 1,1 voire (s'il fallait inclure le crâne de Taung) 0,8 MA environ.

Le genre *Homo* sera-t-il bientôt reconnu jusqu'à 3,5 et 4 MA dans la région d'Hadar et à Kanapoi? Ce n'est pas impossible. Pour l'instant *H. habilis*, la plus ancienne espèce assez généralement acceptée du genre concerné, est du moins limitée au gisement de Sterkfontein (avec notamment l'ensemble Sts 53), et trois gisements de l'Est (Groupe G-H de l'Omo, Est Turkana et Lit I-II d'Olduvai): ils s'échelonnent de ca 2 à 1,6 MA. *H. erectus* apparaît quant à lui relayer la forme *habilis*, puisqu'on le date de 1,6 MA dans l'Est Turkana et à Olduvai, de 1,5 MA à Melka-Kunturé (Ethiopie) et de 1,2 dans l'Omo. Il pourrait se maintenir jusqu'il y a moins de un demi-million d'années en Tanzanie. Il est à propos de rappeler que les gisements les plus anciens hors d'Afrique étaient datés de 1,7 MA (Djetis, Indonésie) et que les plus récents (Choukoutien, Chine) sont estimés à 0,45 MA: les deux dates encadrent donc assez bien la durée reconnue pour l'Afrique.

REDRESSEMENT POSTURAL ET ANATOMIE

Le redressement du primate est un phénomène aux multiples incidences anatomofonctionnelles. Il est conditionné par et rejaillit sur l'entièreté du système considéré: il n'y a guère de structure qui ne s'en trouve plus ou moins profondément modifiée, dans le jeu d'une étroite interdépendance de tout l'organisme. Au niveau du squelette pourtant — et il constituera souvent le seul document objectif directement utilisable — certaines régions sont plus significatives et autorisent des conclusions plus sûres. Ainsi le matériau paléontologique susceptible d'informer sur les conditions posturales concerne bien évidemment directement le bassin, l'extrémité postérieure (fémur, tibia, tarse et métatarse), le sacrum et la colonne vertébrale; mais secondairement aussi le rapport des membres antérieur et postérieur, et davantage encore le crâne, en particulier le *foramen magnum*, la région nuchale et la projection faciale (Washburn, 1978).

Les éléments postcrâniens du squelette hominidé actuellement disponibles ont été abondamment multipliés dans les récentes années, à l'occasion notamment des fouilles pratiquées dans l'Est africain et il n'est sans doute pas possible d'en fournir une liste parfaitement à jour. Quelques pièces plus importantes ont permis des observations et des études précises qui fondent les remarques qu'on va proposer plus bas.

A. *Le pelvis*

L'examen du pelvis d'*Australopithecus* et des premiers *Homo* a donné depuis une dizaine d'années lieu à une série de travaux. Robinson (1972), Zihlman et Hunter (1972), Lovejoy, Heiple et Burnstein (1973), Zuckerman *et al.* (1973), Oxnard (1975) ont tous reconnu la locomotion bipède en ces deux formes, mais l'ont associée de nuances diverses et leurs avis ne laissent pas de s'opposer ou de se contredire partiellement. Pour les uns, il n'y a pas de différence entre la locomotion des deux espèces d'*Australopithecus*, l'une et l'autre suffisamment adaptée au bipédalisme. D'autres reconnaissent à *A. africanus* une efficacité de vélocité, à *A. robustus/boisei* une adaptation parallèle au grimpement et donc à l'habitat arboricole. La pleine efficacité de la marche est mise en doute par Zihlman et Hunter (1972) tandis que Zuckerman et Oxnard insistent plutôt sur une marche d'allure *différente* de celle de l'homme moderne.

La documentation, jusqu'il y a peu tout compte fait fort lacunaire, a été récemment complétée par un nouveau bassin en provenance de Swartkrans, suggérant un réexamen fondamental du matériau. C'est ainsi que huit ou neuf pièces constituent aujourd'hui la collection des pelvis hominidés du Plio-Pleistocène inférieur. Il s'agit des specimens MLD 7 et 8, respectivement ilium gauche et ischium droit d'un adolescent, appartenant peut-être au même individu et attribués traditionnellement à *A. africanus*; de MLD 25, ilium gauche fragmentaire de la même espèce. Sts 14, *A. africanus* lui aussi et sensiblement plus jeune, en provenance de la brèche inférieure de Sterkfontein, représente un pelvis adulte virtuellement complet, associé aussi bien à deux vertèbres sacrées et à une quinzaine d'autres vertèbres en succession sur le même rachis. Du même gisement encore, Sts 65, portion d'un ilium droit et du pubis correspondant, appartenant à un *A. africanus* adulte.

La brèche osseuse de Swartkrans et celle de Kromdraai ont fourni un os coxal droit (SK 50) et un ilium gauche (TM 1605), tous deux adultes, généralement attribués à la forme *boisei* (*Paranthropus*). Le specimen SK 3155, de Swartkrans, daté de 1,5 à 2,5 MA est attribué par les uns à *H. erectus* (Brain, Vrba et Robinson, 1974), par les autres (McHenry et Corruccini, 1978) à la forme *boisei*. AL 288-1 enfin, le squelette à moitié complet découvert dans l'Hadar, possède les deux os coxaux entre autres éléments. Il sont provisoirement attribués à *H. habilis*. OH 28 est un autre os coxal, d'*H. erectus* (Day, 1971).

Au sein de ce matériel, trois pièces adultes plus complètes méritent un examen plus approfondi et permettent d'utiles comparaisons: elles ont notamment été soumises à une analyse multivariée, impliquant 568 autres bassins appartenant à quelque 22 genres modernes de primates humains et non-humains. Il s'agit de OH 28, SK 3155 et Sts 14. Steudel (1978) y a repéré certaines différences anatomiques d'avec l'homme moderne, entre autres l'orientation différente de la portion antérieure de la lame iliaque et la profondeur de l'ischium. Mais il semble qu'on n'en puisse pas déduire aucune indication concernant une moindre efficacité locomotrice chez les formes fossiles concernées, *erectus*, *africanus*, voire *robustus/boisei*. McHenry et Corruccini (1978) par une voie analogue, mais étendue à MLD 7 et MLD 25, soulignent de leur côté les différences fondamentales qui opposent les bassins fossiles hominidés des formes pongidées de référence et, au contraire, leur commune proximité des formes humaines récentes de comparaison. Les caractéristiques particulières de Sts 14, pour réelles qu'elles soient, ne sauraient masquer la ressemblance fondamentale avec *Homo* dont il est phénétiquement tout proche. Lovejoy (1976) estime que s'il existe sans doute chez l'homme moderne certaines caractéristiques qui ne le confondent pas avec les Hominidés primitifs, elles ne concernent pas le type de locomotion ou de redressement, mais certaines spécialisations de l'articulation de la hanche entraînées par la nécessité de mettre au monde des foetus à crâne notablement plus volumineux.

B. *Le fémur*

Le fémur constitue manifestement un des éléments anatomiques importants dans l'appréciation du type locomoteur des primates hominidés. Aussi a-t-il été abondamment étudié, plus récemment entre autre par Wolpoff (1978), Corruccini et McHenry (1978 et 1980). Le matériau disponible est toutefois limité et son interprétation est rendue particulièrement délicate du fait de son caractère fragmentaire et de l'impossibilité aussi qu'il a souvent à associer les divers éléments exhumés (tête, col, diaphyse ou extrémité distale) entre eux d'une part, avec le bassin ou le tibia correspondant de l'autre, ou davantage encore avec les crânes ou dentitions, fondements essentiels de la taxinomie. Dans un certain nombre de cas plus favorables pourtant, les circonstances de la fouille ou la localisation stratigraphique permettent d'attribuer avec suffisante certitude les pièces

TABLE 1

Nº du specimen	Nature du fragment	Origine	Espèce probable
AL 128-129		Hadar	*A. afarensis*
AL 288-1	Portion de fémur	Hadar	*A. afarensis*
KNM-ER 1500	Squelette fragmentaire	Est Turkana	
KNM-ER 1503	Extrémité proximale fémur	Est Turkana	*A.* sp.
KNM-ER 1505	Tête, col, diaph., partie distale fémur g.	Est Turkana	*A.* sp.
KNM-ER 1822	Fragment diaph. fémur	Est Turkana	*A.* sp.
Sts 14	Extrémité prox. fémur g.	Sterkfontein	*A. africanus*
Sts 34	Extrémité distale fémur dr.	Sterkfontein	*A. africanus*
TM 1513	Extrémité distale fémur g.	Sterkfontein	*A. africanus*
KNM-ER 993	Extrémité distale fémur	Est Turkana	*A. boisei*
KNM-ER 738	Tête fémorale	Est Turkana	*A. boisei*
SK 82	Extrémité proximale fémur	Swartkrans	*A. robustus/boisei*
SK 83	Extrémité proximale fémur	Swartkrans	*A. robustus/boisei*
SK 97	Extrémité proximale	Swartkrans	*A. robustus/boisei*
KNM-ER 803	Diaphyse fémur gauche	Est Turkana	*Homo* sp.
KNM-ER 1472	Fragment fémoral	Est Turkana	*Homo* sp.
KNM-ER 1481	Fragment fémoral	Est Turkana	*Homo* sp. ou (?) *A. africanus*

fémorales à telle ou telle des quatre ou cinq espèces hominidées concernées. C'est ainsi que les analyses ont pu habituellement considérer une quinzaine de pièces, dont on propose ici la liste, avec indication de la succession chronologique probable et l'attribution spécifique présumée.

Ces diverses pièces sont toutes significativement différentes des fémurs actuels d'*Homo sapiens*: la longueur du col en particulier est manifestement supérieure chez les formes australopithèques. Pour Lovejoy *et al.* (1973), il s'agirait là d'une situation de l'abducteur réduisant la pression exercée sur la tête fémorale chez les Hominidés primitifs. Avec l'augmentation du volume crânien du foetus à naître, cette disposition aurait été progressivement abandonnée (Corruccini et McHenry, 1980).

Par ailleurs *A. robustus/boisei* et *Homo* sont, à deux MA d'années d'ici, distincts les uns des autres sur la base du fémur, et probablement différents aussi d'*A. afarensis* et *africanus*. C'est la forme *boisei* qui paraît toutefois le moins proche de la forme moderne *sapiens*, au point qu'on est en droit de reconnaître deux types morphologiques distincts: le premier (*A. afarensis*, *A. africanus* et *Homo* sp.) plus semblable à *H. sapiens*, l'autre (*A. boisei*) nettement particulier. Les deux types impliquent-ils des différences mécaniques et locomotrices? C'est possible, mais dans l'ignorance où nous sommes d'un type de progression bipédale différent de celui de l'homme moderne, il n'est guère possible de matérialiser ou de concrétiser cette possibilité.

C. *Le pied*

Les documents paléontologiques concernant le pied des premiers hominidés du Plio-Pleistocène sont très pauvres. En Afrique du Sud, seuls quelques éléments ont été signalés, en provenance de Kromdraai, attribuables sans doute à la forme robuste d'Australopithèque: un astragale incomplet (TM 1517) et deux phalanges. KNM-ER 803 et 1500, de l'Est Turkana comportent quelques os du pied, mal connus encore; pareillement AL 288-1 de la région d'Hadar. Un document beaucoup plus éclairant, mais unique, est disponible depuis la découverte, en 1960 à Olduvai, de la plus grande partie d'un pied gauche attribué à *Homo habilis*. Présenté par Leakey (1960), le pied a été étudié notamment par Day *et al.* (1964 et 1968), Lisowski *et al.* (1974 et 1976), Oxnard et Lisowski (1980). L'allure du talus paraît sensiblement différente de la morphologie correspondante chez *H. sapiens*. Par ailleurs la restitution de la voûte du tarse ne paraît pas aboutir à une arche analogue à celle du pied humain actuel. La bipédie de l'hominidé d'Olduvai suggérerait plutôt, dans l'allure de la sole plantaire, la disposition du pied telle qu'elle est manifestée par le chimpanzé et le gorille, lorsqu'ils marchent en situation redressée...

D. *Les proportions des membres*

Parmi les primates actuels, le rapport des longueurs des membres antérieur et postérieur est caractéristique des différents types locomoteurs propres à chacun d'entre eux: bipède, brachiateur, semibrachiateur ou quadrupède. Il n'est donc pas sans intérêt d'interroger à cet endroit la situation particulière des quelques associations d'os des membres découvertes parmi les hominidés fossiles. L'étude a été faite à plusieurs reprises, notamment par Robinson (1972) et McHenry (1978). C'est dans l'Est Turkana que pareilles associations sont les plus riches d'enseignement. Il s'agit des individus KNM-ER 803, 1500 et 1503-4. On peut en rapprocher TM 1517 de Kromdraai et AL 288-1 de la région d'Hadar. Il ressort de l'analyse ainsi pratiquée que la forme la plus tardive appartenant au genre *Homo* (KNM-ER 803) et datée de 1,5 MA, présente un rapport membre antérieur/membre postérieur typiquement « humain », voire même *sapiens*. Au contraire les proportions des formes plus anciennes, australopithèques, deviennent toutes des valeurs correspondantes de *Homo* par quelque 20%, et se présentent comme intermédiaires entres les singes anthropoïdes et *Homo sapiens*, généralement plus proches toutefois de ce dernier. Les membres supérieurs sont relativement plus longs, les membres inférieurs plus courts que chez l'homme actuel. On en parfois déduit des implications locomotrices, par exemple en inférant que le membre supérieur plus développé pouvait intervenir dans le déplacement, soit par *knuckle-walking* (Howell et Wood, 1974), soit par pratique du *tree-climbing* (Oxnard, 1975; Ciochon et Corruccini, 1976). Sans qu'on puisse exclure formellement ces éventualités, il est sans doute plus raisonahle d'admettre que, si la bipédie des Australopithèques n'a pas encore entraîné la réduction du membre supérieur, c'est que la pression de sélection adaptative s'est exercée plus faiblement à son niveau qu'à celui du membre inférieur. Car il est essentiel de reconnaître qu'aucun élément du squelette appendiculaire postérieur présentement connu ne fournit d'argument s'opposant à une bipédie habituelle des Australopithèques.

REDRESSEMENT ET CONDITIONS ECOLOGIQUES

Déplacement du centre de gravité du primate, modification de la fonction du muscle *gluteus maximus* par altération du rapport des longueurs de l'ischium et du membre inférieur permettant un mouvement plus rapide et une locomotion plus efficace, amélioration aussi de la balance du corps par réorientation et nouvelle architecture des écailles iliaques: telles sont quelques caractéristiques de la locomotion bipède *habituelle* de l'homme, comparée à la fonction locomotrice propre aux pongidés. Selon Robinson, Freedman et Sigmon (1972), ces adaptations hominidées n'ont pas eu lieu de manière synchrone. Les diverses espèces d'Australopithèques manifestent bien la réorientation occipitale, la courbure typiquement humaine du rachis, l'élargissement du sacrum, l'ilium trapu et déployé vers l'arrière; elles ont un certain contrôle de la balance latérale, l'orientation de l'ischium et le type d'insertion glutéale voisin. Mais les formes robuste et gracile diffèrent, nous dit-on, à propos de la longueur relative de l'ischium et du membre inférieur. Il en résulterait que l'acquisition d'un mécanisme d'efficacité et de vélocité dans la progression n'a pas été synchrone chez *A. robustus/boisei* avec les autres modifications aboutissant à la bipédie. On en conclut que l'acquisition de la locomotion bipède se serait effectuée en deux phases: la première comme adaptation aux conditions de vie en milieu boisé, l'autre impliquant la modification du mécanisme locomoteur pour un déplacement en vélocité et correspondant à une adaptation au biotope de savane sèche.

Ce schéma ingénieux rend peut-être compte des observations anatomiques et climatiques concernant les Australopithèques du Sud africain, telles qu'elles nous parviennent des cinq grottes du Transvaal. Mais on se permet de penser qu'il est moins aisément applicable aux conditions de l'Est africain, de la Tanzanie aux Afars. Sans doute la même coexistence des formes primitives, gracile et robuste d'Australopithèque se présente-t-elle aux Afars, dans l'Omo, au Kenya ou en Tanzanie avec des dates somme toute compatibles avec celles de l'Afrique du Sud (encore que partiellement étendues vers le bas pour le Kenya). Mais les biotopes caractéristiques des diverses formes semblent sensiblement différents d'un bout à l'autre du continent aux époques concernées. Si ces différences peuvent sans doute se comprendre dans le cadre d'une certaine adaptabilité des formes en question, on voit moins qu'elles puissent en même temps constituer un mécanisme explicatif de l'acquisition des diverses modalités locomotrices de la progression bipède.

L'influence du climat sur l'origine et la diversification des primates supérieurs et le rôle des contrastes saisonniers progressivement exprimés à partir du Tertiaire est vigoureusement mis en lumière depuis quelques années. Proportions générales, régime alimentaire, comportement sensoriel voire locomoteur, et leur évolution des prosimiens aux Anthropoïdea ne semblent pas sans dépendance des modifications climatiques et biotopales affectant, au cours du Cénozoïque et selon une profondeur progressivement accrue, les continents africain et eurasiatique. Les travaux de Chivers (1972), Radinsky (1974), Tuttle (1972), Cachel (1979) et d'autres ont interprété dans ce sens les fluctuations climatiques plus considérables de la fin du Tertiaire et du Pleistocène. Il ne semble pas douteux qu'une certaine influence des climats a pu s'exercer sur les divers groupes de primates en évolution. Il est moins aisé de déterminer la manière dont ils ont influé ou les mécanismes par lesquels ils pourraient devoir être tenus responsables du processus diversifiant et notamment des spécialisations locomotrices attachées au phénomène d'hominisation. Il y a donc lieu, dans le cadre de cette note, de s'interroger en particulier sur les biotopes africains des gisements à Hominidés du Plio-Pleistocène.

Les nombreux travaux développés depuis une trentaine d'années, tant autour des gisements du Transvaal qu'à propos de ceux de la *Rift Valley* et de la région des Afars, ont permis de restituer avec assez de précision les biotopes particuliers des différents hominidés africains des niveaux pre-*sapiens*. Etude des pollens, des associations faunistiques de l'Omo, d'Olduvai et des brèches à Australopithèques, étude des micromammifères, des ostracodes et des mollusques, analyses sédimentologiques: autant de techniques mises en oeuvre, grâce auxquelles les divers milieux sont mieux connus, habités par les Hominidés fossiles. Les grossières séquences climatiques d'il y a trente ans ont fait place à un spectre beaucoup plus affiné de la diversité climatique du Cap aux Afars, et de la transformation diachronique subie dans les diverses régions au cours des 4 à 6 millions d'années considérés. Ce n'est pas le lieu de reproduire ici dans le détail ces études fouillées et souvent brillantes, mais d'en résumer sobrement les conclusions essentielles.

Et dans l'Est africain d'abord: les gisements qui ont livré *Australopithècus afarensis* et *africanus* correspondent ici dans leur ensemble à des biotopes plus couverts, sinon boisés: savane plus ou moins touffue à Lukeino (6,5 MA), savane humide ou forêt épaisse à Lothagam (6-4 MA), Kanapoi (4 MA) ou Chemeron (3,2 MA), savane à acacias, fourré épais ou prairie ouverte que l'alternance des saisons fait tantôt humide, tantôt semi-aride à Laetolil (3,6 MA), savane couverte proche de la forêt à Hadar (3 MA): tels sont les paysages occupés par *A. afarensis*. Même la formation de Kubi Algi et la base de Koobi Fora, dans l'Est Turkana, suggèrent des conditions plus humides que les niveaux supérieurs de Koobi Fora et d'Ileret. Ce sont encore substantiellement les conditions qui affectent un peu plus tard, dans l'Omo et l'Est Turkana, les biotopes fossilisés dans les gisements où l'on retrouve *A. africanus*, à partir de 2,9 MA.

Un changement climatique franc semble alors intervenir vers les 2,3 MA (Cerling *et al.*, 1977): il est particulièrement mis en lumière dans le bassin de l'Omo et se caractérise par une brusque dessication, repérée d'ailleurs parallèlement dans les couches supérieures de Koobi Fora et d'Ileret de l'Est Turkana, et retrouvée aussi bien à travers toute la séquence d'Olduvai: précisément les couches qui ont livré *Australopithecus boisei* et *Homo habilis*. Coppens (1977 et 1979) reconnaît que les conclusions définitives doivent encore être réservées, mais il estime qu'« il semble bien que les espèces graciles d'Australopithèque se rencontrent plus volontiers associées (dans l'Est africain) à des milieux humides, couverts, voisins de forêts et que les espèces robustes apparaissent ou persistent au moment où cette humidité diminue. *Homo habilis* arrive lui-même, ou tout au moins se développe en même temps que la sécheresse et vit aux côtés d'*A. boisei* ».

En Afrique du Sud par contre, les gisements sont moins aisément datables. L'analyse des brèches et l'examen des associations faunistiques ont pourtant très extensivement renseigné sur les climats au moment de leur formation. On s'accorde généralement aujourd'hui sur la succession chronologique Makapansgat, Sterkfontein, Swartkrans, Kromdraai et Taung, la brèche la plus ancienne remontant à quelque 3 MA (peut-être plus de 3,2 MA, selon Tobias, 1973), la plus récente pouvant ne pas remonter au delà d'un million voire 0,8 MA. Les biotopes concernés attestent un paysage ouvert, occasionnellement boisé, jamais une forêt au sens vrai du terme. Par comparaison aux conditions actuelles, le climat a dû évoluer du très sec (à Makapansgat) vers du moins sec (à Sterkfontein et Swartkrans), pour voir finalement dominer (à Kromdraai) des conditions nettement plus humides que présentement.

Il ne semble pas possible de mettre en parfait parallèle les données climatiques de l'Est et du Sud de l'Afrique, en tous les cas pour ce qui concerne *A. robustus/boisei*. Tandis qu'il évolue là-bas dans un biotope récemment marqué par une brusque dessication, il semble s'accomoder ici, un peu plus tard il est vrai, d'un environnement nettement plus humide. Si ces données ne sont pas contradictoires, compte tenu d'une adaptabilité plus ou moins considérable de l'organisme, il est du moins difficile de préciser dans quel sens la modification climatique a positivement influencé la diversification des Hominidés à l'échelon *Australopithecus*.

Au demeurant VRBA (1975), Hay (1976), Boaz et Howell (1977) rappellent-ils à propos qu'il est actuellement établi que les Australopithèques du type robuste et les premiers représentants du genre *Homo* coexistent en Afrique orientale dans un climat semi-aride. Mais leur coexistence pourrait bien décidément être également établie dans des climats plus humides (Peters, 1979) et il n'y a sans doute pas de *relation simple et directe* entre morphologie, c'est à dire taxinomie des premiers Hominidés, et circonstances climatiques (Boaz, 1977; Butzer, 1977 et Klein, 1977).

Il y a près de vingt ans que Napier (1964), sur la base du matériel sud-africain, s'attachait aux différences anatomiques entre les divers éléments anatomiques responsables de la bipédie *habituelle* chez les Australopithèques gracile et robuste. Il en déduisait deux types distincts de locomotion: tandis que la forme gracile bénéficiait d'une progression rapide, mieux équilibrée, la marche du *robustus* était caractérisée par un certain « waddling », sorte de dandinement, d'allure de canard, foulée courte, traînante, dans un espèce de balancement à pauvre rendement physiologique. Napier suggérait que les deux formes, gracile et robuste, pouvaient s'enraciner dans un ancêtre commun, et que l'évolution d'un même patrimoine génétique avait dès lors été marquée par le biotope davantage boisé ou plus ouvert dans lequel le phylum s'était trouvé. Suffisamment pourvu d'une nourriture toujours disponible, suffisamment protégé par le milieu, le groupe demeuré dans la forêt n'aurait pas éprouvé au même degré la pression sélective favorisant l'accélération du processus d'efficacité locomotrice en économie et rapidité du déplacement; la pression sélective aurait au contraire été déterminante pour le groupe évoluant dans un milieu ouvert, de savane, avec toutes les conséquences au point de vue alimentation, libération des extrémités antérieures et capacité artisanale. Force est aujourd'hui, depuis la reconnaissance des biotopes de l'Est africain (6 à 2,5 MA), de constater que c'est précisément dans un milieu de savane plus ou moins touffue, parfois proche de la forêt, voire de forêt épaisse, qu'on repère les formes *afarensis* et *africanus*, et que la forme *boisei* apparaît au moment de la dessication qui marque ultérieurement la *Rift Valley*.

L'INFORMATION MIO-PLIOCÈNE

Le type primitif de locomotion chez les primates est la quadrupédie dans un habitat arboricole. Les spécialisations brachiatrices, semibrachiatrices et bipédales sont intervenues au cours de l'évolution tertiaire du groupe et c'est donc au cours du Mio-Pliocène qu'on pourrait s'attendre à découvrir les premières manifestations de la station érigée ou des conséquences au niveau du membre postérieur de la spécialisation brachiatrice antérieure.

Il est donc intéressant d'interroger à ce propos les éléments fossiles disponibles, notamment pour le squelette appendiculaire et la ceinture postérieure (a) des Pongidés, et (b) des « Hominidés » tertiaires préalables à l'apparition des Australopithèques, questionnant à ce sujet leur éventuelle séparation d'avec les Cercopithécidés demeurés plus « primitifs ».

A. *Les fémurs hominoïdes*

Quatre fémurs hominoïdes mio-pliocènes ont été récemment soumis par McHenry et Corruccini (1976) à une analyse uni- et multivariée, et comparés à une série de 244 fémurs appartenant à huit formes de Pongidés et Cercopithécidés actuels (*Gorilla*, *Pan*, *Pongo*, *Hylobates*, *Nasalis*, *Prebytis* et *Macaca*). Les quatre fémurs fossiles concernés sont BM *Proconsul* (*Dryopithecus*)? *nyanzae* (Moboko I., Kenya, du Miocène moyen, ca 14 MA); *Pliopithecus* (*Epipliopithecus*) *vindobonensis* I (Neudorf a.d. March, Tchécoslovaquie, Miocène moyen basal ou Helvétien); le fémur d'Eppelsheim (*Hylobates fontani* OWEN, *Dryopithecus*? cf *D. fontani* de Simons et Pilbeam, 1965, Pliocène inférieur); KNM-SO 1011,? *Limnopithecus macinnesi* (Songhor, Kenya, 20 MA).

De cette étude il résulte qu'il n'y aurait pas de relation évolutive directe des Dryopithèques, très proches encore de *Nasalis*, à aucun des Pongidés actuels d'Afrique. La structure fondamentalement cercopithecoïde, c.à.d. non spécialisée, des fémurs hominoïdes tertiaires indique que les Hominoïdes actuels ont dû apparaître par évolution parallèle au delà du Miocène moyen, ou via un ancêtre commun postérieur. Rien n'indique du moins, à cette époque de l'évolution des Primates, une quelconque préparation du redressement postural au sein du complexe dryopithèque.

B. *L'Oréopithèque*

Oreopithecus bambolii (Miocène terminal - Pontien, 14-12 MA) a parfois été proposé comme premier candidat à la station érigée. Le squelette postcrânien en particulier ne laisse pas de présenter certaines particularités (morphologie des côtes et largeur du thorax, nombre et structure des vertèbres lombaires, écaille iliaque) qui ont permis parfois de suggérer une spécialisation bipède. En réalité les études plus fouillées ont démontré plutôt une morphologie franchement hominoïde généralisée, plus proche peut-être de ce fait de certaines structures hominidées que des pongidés modernes évolués (Straus, 1962). Mais essentiellement brachiateur et arboricole, *Oreopithecus* n'entre plus en ligne de compte pour un quelconque processus d'hominisation. Il n'est sans doute pas exclus qu'il aît occasionnellement risqué des incursions sur le sol, mais la bipédie ne saurait être structurelle et il faut donc chercher ailleurs les préparations phylétiques du redressement postural des Australopithèques.

C. *Le Ramapithèque*

Créé par Lewis (1934) pour un fragment de maxillaire du Miocène supérieur de la formation de Nagri dans les Siwaliks, le genre *Ramapithecus* occupe, depuis sa révision par Simons (1961 et 1964) une place spéciale dans les hypothèses relatives à l'hominisation et au redressement bipédal. Grossi de pièces initialement attribuées par Pilgrim (1910) au genre *Bramapithecus* et de nouvelles découvertes en Inde et au Pakistan, le genre *Ramapithecus* s'est progressivement vu attribué le *Kenyapithecus wickeri* Leakey 1962, le *Graecopithecus freyburgi* von Koenigswald 1972, le *Sivapithecus alpani* Tekkaya 1974, le *Rudapithecus hungaricus* Kretzoi 1975 et, plus récemment, des pièces découvertes à Pasalar, en Turquie (Andrews et Tobien, 1977) et à Lufeng, dans le Yunnan (Xu et Lu, 1979).

Réparti ainsi de l'Est-africain à l'Europe centrale, au Proche-Orient, à l'Himalaya et jusqu'aux extrémités de l'Asie, la forme *Ramapithecus* appartient au Miocène moyen ou supérieur, voire à la limite inférieure du Pliocène, datée de 15 à 8 MA environ. On s'accorde généralement à reconnaître aux pièces attribuées au genre *Ramapithecus* une série de caractères les distinguant à la fois des diverses formes dryopithèques et des Pongidés modernes. D'aucuns (p. ex. de Bonis, 1981) estiment que cette constellation, pour réelle qu'elle soit, n'autorise pourtant pas l'individualisation du genre en un taxon particulier. Certains (Genet-Varcin, 1980) se sentent peu disposés à y voir les premiers représentants de la famille des Hominidés. Pourtant de très nombreux spécialistes estiment de leur côté que *Ramapithecus* « paraît confirmer l'existence d'une radiation de primates hominoïdes à l'intérieur de laquelle s'enracinent sans doute les Hominiens Plio-Quaternaires » (de Bonis, 1981).

Le genre *Ramapithecus* ainsi reconsidéré depuis 20 ans est donc repéré aujourd'hui en plus de douze gisements:

— en Afrique, dans l'île de Moboko et à Kathwanga (I Rusinga, Lac Victoria); au Lac Baringo, à Ngorora et Lukeino, à Fort Ternan;

— en Asie, dans les Siwaliks (au Nord de l'Inde, à Haritalyangar; à Domali, plateau de Potwar, dans le Pakistan; à Candir, près de Ankara, en Turquie; à Lufeng, dans le Yunnan, en Chine;

— en Europe, à Pyrgos (Grèce) et Rudabanya (Hongrie).

En réalité les quelque 150 spécimens actuellement disponibles représentent presque exclusivement des fragments maxillaires et mandibulaires ou des dents isolées. Aucun crâne tant soit peu significatif, aucun élément du squelette postcranien interprétable n'a été publié qui permette de préciser à ce moment les adaptations locomotrices et posturales de *Ramapithecus*, même si Pilbeam *et al.* (1979) annoncent des découvertes dans ce sens dans le Pakistan septentrional. L'attribution de *Ramapithecus* à la famille des Hominidés est justifiée, par les paléontologistes qui la suggèrent, sur la base de la structure dentaire (épaisseur de l'émail, usure interstitielle et gradient d'attrition molaire) et du contour alvéolaire, ou de la fosse canine. La référence à une éventuelle bipédie ne saurait être que très conjecturale ou imposée par le contexte écologique.

L'assemblage le plus considérable et le plus représentatif provient des sédiments miocènes du plateau de Potwar, au Pakistan. La faune permet de reconstruire une série d'habitats divers, échelonnés depuis la plaine côtière au climat subtropical, jusqu'à la savane élevée, au climat plus sec où les pluies saisonnières rappellent l'environnement actuel. La végétation comportait ici une forêt d'essences caduques, là un maquis, plus loin une savane herbeuse (Simons, 1979) avec prédominance de biotopes ouverts (Tattersall, 1969; Tattersall et Prasad, 1971). C'est dans cet environnement que l'on retrouve *Ramapithecus*, un primate léger, de quelque 40 livres sans doute. Là où il est repéré, les conditions climatiques paraissent moins humides, les plantes fossiles de type moins tropical: ce qui permet de penser que ces hominoïdes ont dû s'accomoder d'une nourriture plus grossière, faite de racines, de rhizomes ou de bambous, ainsi que le suggère d'ailleurs l'épaisseur remarquable de la couche d'émail de la dent. L'environnement, le régime alimentaire et la taille ne sont donc plus tout à fait inconnus. Est-il vraisembable que *Ramapithecus* aît possédé « un vaste répertoire de gestes, de cris pour la communication? Qu'il aît constitué des groupes sociaux importants »? (Simons, 1979) le pensent qui affirment même qu'il commençait à se grouper de façon humaine. Ceci nous paraît provisoirement encore du domaine conjectural; conjecturale aussi l'acquisition d'une quelconque bipédie, sinon occasionnelle, à la façon dont on la repère aujourd'hui chez les chimpanzés, soit pour l'attaque, soit pour le transport de nourriture. L'écosystème ne laisse pas de façonner l'individu biologique qui lui est intimement lié, et il est donc possible que sur cette forme du Miocène terminal nous puissions demain vérifier de fait les premières manifestations du redressement postural à venir. Les postuler à ce niveau semble, aujourd'hui du moins, une extrapolation par trop hardie.

CONCLUSIONS

Au terme de ce rapide survol des données actuellement disponibles en paléoanthropologie, on peut sans doute résumer en quelques propositions l'état présent des connaissances en matière d'acquisition de la station érigée et de la locomotion bipède:

1. La *bipédie habituelle* est acquise dans le groupe hominidé dès le stade australopithèque, soit il y a au moins 3 MA, tant pour *A. afarensis* et *africanus* que pour *A. boisei.*

2. Les différences anatomiques repérées entre les diverses formes fossiles et l'homme actuel souffrent des interprétations sensiblement distinctes. Ces différences ne sont pas nécessairement l'indication d'une moindre efficacité ou d'un moindre achèvement de la fonction locomotrice: elles pourraient ne traduire qu'un *autre* type de progression bipédale, dont il est aussi bien difficile d'imaginer le modèle

3. Les différences repérées entre les formes australopithèques sont comprises par certains comme l'indication d'une évolution plus efficace du groupe gracile, dans le sens de la rapidité et de l'équilibre du déplacement.

4. Antérieurement aux Australopithécinés, on ne possède aujourd'hui aucun document objectif permettant de situer les circonstances de l'apparition du redressement.

5. Les Hominoïdes miocènes du complexe dryopithèque possèdent encore une structure généralisée, fondamentalement cercopithécoïde et se situent très certainement plus haut dans le temps que toute spécialisation brachiatrice ou bipède.

6. *Oreopithecus* est déjà fondamentalement brachiateur: il est marginal par rapport au processus d'hominisation, sans qu'on puisse exclure une *bipédie occasionnelle.*

7. *Ramapithecus* demeure un candidat valable pour les premières manifestations du redressement postural hominidé. Les éléments actuellement recouvrés du squelette sont impropres à confirmer ou infirmer l'hypothèse d'une éventuelle bipédie à ce niveau.

8. De toute manière, un hiatus considérable de quelques millions d'années demeure, 3 à 6 MA selon les estimations, entre *Ramapithecus* et les premiers Australopithèques. C'est dans cet intervalle de temps que l'on doit s'attendre à retrouver les fossiles susceptibles d'éclairer le débat. La région du Lac Baringo (Lothagam et Lukeino) se présente comme parti-

culièrement favorable puisqu'elle a fourni *à la fois* les plus anciens Australopithèques *et* le Ramapithèque.

9. Les modèles écologiques tant travaillés depuis quelques années doivent encore être précisés: dans l'état actuel de nos connaissances, leur fécondité explicative des spécialisations locomotrices manque encore de l'universalité suffisante pour pouvoir justifier adéquatement les circonstances du redressement postural des Hominidés.

BIBLIOGRAPHIE

Andrews P. and Tobien H., *New Miocene locality in Turkey with evidence on the origin of Ramapithecus.* « Nature », *268*, 699-701 (1977).

Boaz N.T., *Paleoecology of early Hominidae in Africa.* « Kroeber Anthropology Soc. Papers », *50*, 36-62 (1977).

Boaz N.T. and Howell F.C., *A gracile Hominid cranium from Upper member G of the Shungura formation, Ethiopia.* « Amer. J. Phys. Anthrop. », *46*, 93-108 (1977).

Brain C.K., Vrba E.S. and Robinson J.T., *A new hominid innominate bone from Swartkrans.* « Ann. Transv. Mus. », *29*, 55-63 (1974).

Butzer K.W., *Environment, Culture and human Evolution.* « Amer. Scient. », *65*, 572-584 (1977).

Cachel S., *A paleoecological model for the origin of higher Primates.* « J. Hu. Evol. », *8*, 351-359 (1979).

Cerling T.E., Hay R.L. and O'Neil J.R., *Isotopic evidence for dramatic climatic changes in East Africa during the Pleistocene.* « Nature », *267*, 137-138 (1977).

Chivers D.J., *The Siamang and the Gibbon in the Malay peninsula.* « Gibbon and Siamang », *1*, 103-135 (1972).

Ciochon R.L. and Corruccini R.S., *Shoulder joint of Sterkfontein* Australopithecus. « Sth. Afr. J. Sci. », *72*, 80-82 (1976).

Coppens Y., *Les Hominidés du Pliocène et du Pleistocène d'Ethiopie, chronologie, systématique, environnement.* In: « Colloque Singer Polignac *Les Origines humaines et les époques de l'intelligence* ». Paris, Masson, p. 79-106 (1977).

Coppens Y., *Les Hominidés du Pliocène et du Pleistocène de la Rift Valley.* « Bull. Soc. Géol. Fr. » (7) XXI, *3*, 313-320 (1979).

Corruccini R.S. and McHenry H.M., *Relative femoral head size in early Hominids.* « Amer. J. Phys. Anthrop. », *49*, 145-148 (1978).

Corruccini R.S. and McHenry H.M., *Hominid femoral neck length.* « Amer. J. Phys. Anthrop. », *52*, 397-398 (1980).

Day M.H., *The Omo human skeletal remains.* « UNESCO, Ecol. and Conservation », *3*, 31-35 (1971).

Day M.H. and Napier J.R., *Fossil foot bones.* « Nature », *201*, 969 (1964).

Day M.H. *et al.*, *Functional affinities of the Olduvai Hominid 8 talus.* « Man », *3*, 440-455 (1968).

de Bonis L., *Les primates hominoïdes du Miocène et le problème du Ramapithèque.* Coll. Intern. CNRS, N° 599. *Les Processus de l'Hominisation*, 49-53 (1981).

Genet-Varcin E., *Les Hommes fossiles.* Paris, Boubée (1980).

Hay R.L., *Environmental setting of hominid activities in Bed I, Olduvai Gorge.* In: « Human Origins ». G. Ll. Isaac and E.R. McCown, eds., pp. 209-225. Menlo Park, A. Staples Press (1976).

Johanson D.C. and White T.D., « Science », *207*, 1104 (1980).

Johanson D.C., White T.D. and Coppens Y., *A new species of the genus* Australopithecus (Primates: Hominidae) *from the Pliocene of eastern Africa.* « Kirtlandia », *28*, 1-14 (1978).

KLEIN R.G., *The ecology of early man in Southern Africa.* « Science », *197*, 115-197 (1977).

KRETZOI M. *New Ramapithecines and* Pliopithecus *from the lower Pliocene of Rudabanya in North-easthern Hungary.* « Nature », *257*, 578-581 (1975).

LEAKEY L.S.B., *Recent discoveries at Olduvai Gorge.* « Nature », *188*, 1050-1052 (1960).

LEAKEY L.S.B., *A new lower pliocene fossil Primate from Kenya.* « Ann. Mag. Nat. Hist. London », *4, 13, 47*, 689-696 (1962).

LEWIS G.E., *Preliminary notice of new man-like apes from India.* « Amer. J. Sci », *5, 27, 159*, 161-179 (1934).

LISOWSKI F.P., ALBRECHT G.H. and OXNARD C.E., *The form of the talus in some higher Primates. A multivariate study.* « Amer. J. Phys. Anthrop. », *41*, 191-216 (1974).

LISOWSKI F.P., ALBRECHT G.H. and OXNARD C.E., *African fossil tali: further multivariate morphometric studies.* « Amer. J. Phys. Anthrop. », *45*, 5-18 (1976).

LOVEJOY C.O., *The locomotor skeleton of basal Pleistocene Hominids.* « Union Intern. Sc. Préhist. Protohist. », IX Congrès, Nice, Coll. VI, 145-176 (1976).

LOVEJOY C.O., *The origin of Man.* « Science », *211* (4480), 341-350 (1981).

LOVEJOY C.O., HEIPLE K.G. and BURNSTEIN A.H., *The gait of* Australopithecus. « Amer. J. Phys. Anthrop. », *38*, 757-780 (1973).

MCHENRY H.M., *Fore- and Hindlimbs Proportions in Plio-Pleistocene Hominids.* « Amer. J. Phys. Anthrop. », *49*, 15-22 (1978).

MCHENRY H.M. and CORRUCCINI R.S., *Affinities of Tertiary Hominid Femora.* « Folia Primatol. », *26*, 139-150 (1976).

MCHENRY H.M. and CORRUCCINI R.S., *Analysis of the hominoid os coxae by cartesian coordinates.* « Amer. J. Phys. Anthrop. » *48*, 215-226 (1978).

NAPIER J.R., *The evolution of bipedal walking in the hominids.* « Arch. Biol. (Liège) », *75*, Suppl. 673-708 (1964).

OXNARD C.E., *Uniqueness and diversity in human evolution.* Univ. Chicago Press (1975).

OXNARD C.E. and LISOWSKI F.P., *Functional articulation of some hominoid foot bones: implications for the Olduvai (Hominid 8) foot.* « Amer. J. Phys. Anthrop. », *52*, 107-117 (1980).

PETERS C.R., *Toward an ecological model of African Plio-Pleistocene hominid adaptations.* « Amer. Anthrop. », *81* (2), 261-278.

PILBEAM D. *et al.*, *Miocene sediments and faunas of Pakistan.* « Postilla », *179*, 1-45 (1979).

PILGRIM G., *Notices of new mammalian genera and species from the Tertiary of India* « Rec. Geol. Surv. India », *401*, 63-71 (1910).

RADINSKY L.B., *The fossil evidence of anthropoid brain evolution.* « Amer. J. Phys. Anthrop. », *41*, 15-28 (1974).

ROBINSON J.T., *Early hominid posture and locomotion.* Univ. Chicago Press (1972).

ROBINSON J.T., FREEDMAN L. and SIGMON B.A., *Some aspects of pongid and hominid bipedality.* « J. Hu. Evol. », *1* (4), 361-370 (1972).

SIMONS E.L., *The phyletic position of* Ramapithecus. « Proc. Nat. Acad. Sc. », *51* (3), 528-535 (1961).

SIMONS E.L., *The early relatives of Man.* « Scient. Amer. », 50-62 (1964).

SIMONS E.L., *L'origine des Hominidés.* « La Recherche », *10* (98), 260-267 (1979).

SIMONS E.L. and PILBEAM D.R., *Preliminary revision of the Dryopithecin.* « Folia Primatol. », *3*, 81-152 (1965).

STEUDEL K., *A multivariate analysis of the pelvis of early Hominids.* « J. Hu. Evol. », *7*, 583-595 (1978).

STRAUS W.L., *Fossil evidence of the evolution of the erect bipedal posture.* « Clin. Orthop. », *25*, 9-19 (1962).

TEKKAYA I., *A new species of tortonian Anthropoid from Anatolia.* « Bull. Min. Res. Expl. Inst. Turkey », *83*, 148-165 (1974).

TOBIAS P.V., *Implications of the new age of the early South African hominids.* « Nature », *246*, 79-83 (1973).

TUTTLE R.H., *Functional and evolutionary biology of hylobatids hands and feet.* « Gibbon and Siamang », *1*, 136-206 (1972).

VON KOENIGSWALD G.H.R., *Ein Unterkiefer eines fossile Hominoides aus dem Unterpliozän Griechenland.* « Proc. Koninkl. Akad. Wet. », *75* (5), 385-394 (1972).

WASHBURN S.L., *The evolution of man.* « Scient. Amer. », 146-154 (1978).

WOLPOFF M.H., *Some implications of relative biomechanical neck length in hominid femora.* « Amer. J. Phys. Anthrop. », *48*, 143-148 (1978).

XU and LU, *The mandibles of* Ramapithecus *and* Sivapithecus *from Lufeng, Yunnan.* « Vert. Palas. », *17* (1), 1-13 (1979).

ZIHLMAN A.L. and HUNTER W.S., *A biomechanical interpretation of the pelvis of* Australopithecus. « Folia Primatol. », *18*, 1-19 (1972).

ZUCKERMAN S. *et al.*, *Some locomotor features of the pelvic girdle in primates.* « Symp. Zool. Soc. London », *33*, 71-165 (1973).

RECENT ADVANCES IN THE EVOLUTION OF THE HOMINIDS WITH ESPECIAL REFERENCE TO BRAIN AND SPEECH

PHILLIP V. TOBIAS
Department of Anatomy, University of the Witwatersrand,
Johannesburg, South Africa

1. INTRODUCTION: CHANGING CONCEPTS IN HOMINID EVOLUTION

The encyclical (*Humani generis*) of Pope Pius XII, promulgated in 1950, included a small but special section about human evolution. Therein it was taught that the direct creation of the human soul by God pertains to Catholic faith, but that discussion of the origin of the human body might continue among competent scholars (Vollert, 1959). As a result, it could be claimed at the Darwin Centennial Celebration held at the University of Chicago in November 1959, that "...currently, more and more theologians are showing themselves favorable to (evolution)" (J. Franklin Ewing, S.J., 1960). Father Ewing went on to elaborate:

> "One reason for this is extrinsic to the science of theology, but exerting a powerful influence on it. This is the piling-up of evidence, particularly palaeontological, which makes human evolution more and more credible". (*op. cit.*, p. 27)

Ewing, himself, had dug up a fossil Neandertal child skeleton at K'sar Akil in the Lebanon (Ewing, 1947, 1949) and at the Darwin Centennial he drew attention to the fact that in the previous 25 years (i.e. since the discovery of the Taung child, the first found of Africa's early hominids - Dart, 1925), more human fossils had been unearthed than in the whole previous history of the world. Unfortunately, my good friend, Father

Franklin Ewing did not live long enough to see the stockpile of hominid fossils more than double again in less than another 25 years. From Africa alone, the number of *early* hominid individuals represented by fossil discoveries rose from a middle value of 148 in 1959 to a middle value of some 485 in 1982! That is, on a moderate estimate of the number of individuals represented by the bones and teeth recovered, the tally had more than trebled. This excludes fossil man of the more recent period from various parts of Africa.

As Ewing pointed out, the very multiplication of the fossil documents has been compelling the claims for the evolutionary origin of man to be taken more and more seriously. Indeed, it would not be going too far to assert that human evolution is one of the most highly confirmed hypotheses in human biology today: and that human biology makes sense only when studied and understood from an evolutionary perspective.

Earlier concepts of hominid evolution were naive when compared to those that have emerged from the careful study of the more voluminous fossil record now available.

(a) *Brain-size and hominid status*

It was once believed that the critical point in the definition of man was his possession of a disproportionately large brain. Anything which was not so endowed was automatically disqualified from membership of the family of man, the Hominidae. This was the nub of the 25-year-long argument about the systematic status of the Taung child, *Australopithecus africanus*: could it really be admitted to the hominids with a brain-size of between 400 and 500 cubic centimetres? It is now known that the earliest fossils which almost all scholars are agreed should be classified within the Hominidae possessed small brains (fig. 1), no bigger in *absolute* size than those of the extant great apes, chimpanzee and gorilla in Africa and orang-utan in Asia. Other features of their bodily structure — such as the evidence of their upright posture, bipedal locomotion and modest-sized canine teeth — sufficed to qualify them as hominids. It was this realisation that Dart's discovery of the Taung skull and his interpretation of its features forced upon the world of anthropology: that the hominids started out with no greater cerebral endowment, in absolute terms, than that of the living pongids. The growing completeness of the fossil record representing stages more advanced than *Australopithecus* has revealed the progressive increase in brain-size of the hominids over the next two to three million years.

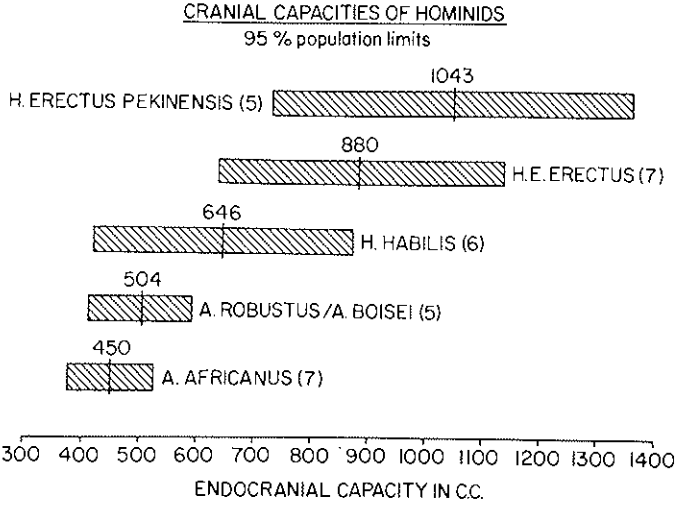
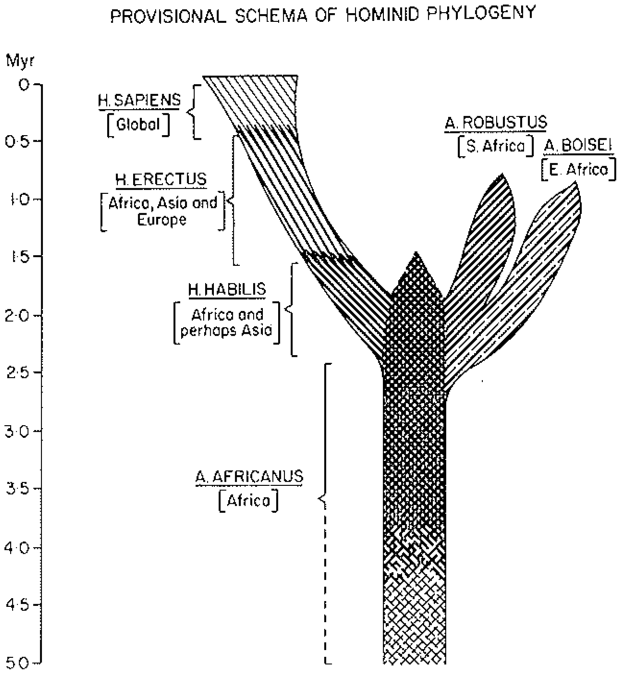


FIG. 1. The means (vertical lines) and 95% population limits of endocranial capacity in five taxa of ancient fossil hominids.

(b) *Ancestral and non-ancestral hominids*

Secondly, 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 palaeontology 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* (fig. 2).



PROVISIONAL SCHEMA OF HOMINID PHYLOGENY

Fig. 2. A schema of hominid phylogeny according to the author's interpretation in 1982. The figures in the left-hand margin refer to the numbers of millions of years (Myr) before the present. The lightly shaded lower part of the trunk of the tree is, in the author's view, occupied by the Hadar and Laetoli fossil hominids for which has been proposed the name *A. afarensis*.

(c) *The extinction of some early hominids*

A third 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 Neandertal man in Europe, namely that it was a side-branch that died out. But the evidence for such suggested Neandertal extinction has never been convincing and Middle European intermediates between Neandertals 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 million years ago (fig. 2). Yet all were good hominids on all accepted classifications.

(d) *The claims of Africa and Asia*

Fourthly, 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 from 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*

Fifthly, 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 in 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 1). 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.

(f) *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 for the australopithecines. In a similar way the Neandertalers of Europe, Asia and North Africa have at various times been classified in a different 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 of the current arguments over the systematic status of various newly-found African fossils are simply the consequence of varying judgments by palaeoanthropologists as to whether the morphology and morphometrics of the new find 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

TABLE 1 — *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 variation (%)
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

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 and describers, tbe accuracy of their measurements, their familiarity with other comparable fossil collections and their morpbological acumen.

(g) *The exaggeration of differences*

A corollary of the last item is that there has been a long-lasting and oft-criticised tendency for discoverers of fossils to tend 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 palaeo-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 palaeo-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 palaeontologists venture into previously unsampled time-levels, it becomes increasingly likely that new taxa may come to light: but the final judgment 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 palaeo-anatomical problem; the *evaluation of the place and significance* of those fossil hominids requires in addition the insights of taphonomy, geochronology, zoogeography, palaeoecology, ethology, taxonomy and, where applicable, archaeology.

(h) *Continuous or discontinuous change?*

An eighth 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 *idée 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 palaeontological 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 million years before present, there is much evidence to suggest that a previously single hominid lineage underwent *cladogenesis* or a splitting into several lineages (fig. 2). 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, the pattern of hominid evolution could be interpreted as illustrating the Eldredge-Gould model of punctuated equilibrium (1972, 1977). In saying this, I do not necessarily support the corollaries of their viewpoint, namely that the main significant steps in evolution take place at branch points and that what happens subsequently is of relatively minor importance. For instance, there is no doubt that the lineage of *Homo* after its cladistic origin underwent most remarkable and significant changes through a sequence of three consecutive chronospecies. 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 c2.3 million years B.P. 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 c1345 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 seems 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, 1975a, 1982a). 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 palaeo-anthropological record, a view that Brace has described as 'bold but unsupported' (1981, p. 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, p. 422). My own studies revealed a reduction in tooth material (summed crown areas of mandibular cheek-teeth) from 787 in *H. habilis* to 485 in modern *H. sapiens* (world-wide inter-population mean): that is a reduction of about 40% on the *H. habilis* value (Tobias, 1981). 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 speciation at punctuating nodal events.

These two lines of metrical evidence show that, since the last major punctuation in hominid evolution (at about 2.3 million years B.P.), phyletic gradualism has been evident in the palaeo-anthropological record. The data lead me to support Brace's claim (1981) that the data of palaeo-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 million years B.P.) 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 hominisation, after the attainment of the upright posture and bipedal locomotion.

We may thus see hominid evolution as proceeding at different rates at different times (fig. 3), a conclusion to which also Cronin *et al.* (1981) have been drawn. It does not provide an illustration of the punctuated

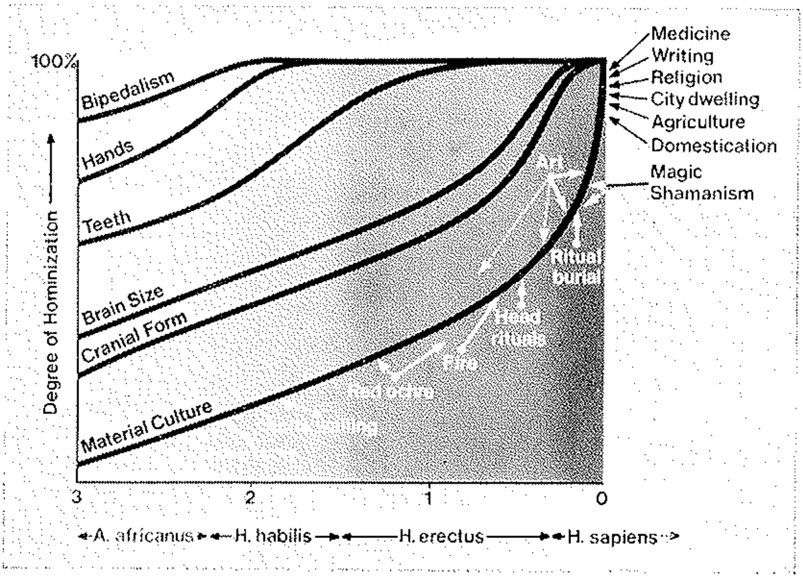


FIG. 3. The pattern of hominization in the last three million years of hominid evolution. For six structural-functional complexes, the tempo of change is shown from least hominized (lower) to most hominized i.e. conforming to the pattern in modern *Homo sapiens* (upper).

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 equibrium. 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), ammonities (Reyment, 1975), trilobites (Henry and Clarkson, 1975) and brachiopods (Ager, 1973).

Perhaps, for terrestrial vertebrates, where emigration and 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, because 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.*, p. 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 states:

> "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, p. 132) and later editions, he adds that neither does 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 4th edition (pp. 359-360), Darwin says, 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 clearly 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 be inextricably interwoven with accelerated change. Darwin envisages periods of change which are not *necessarily* associated with branching events: they may be or they may not be, depending on the individual circumstances of each species. Or, to put it in another way, some instances of modification may arise by branching events with speciation, whilst others may arise gradually, phyletically, without major cladistic phenomena. Thus, Darwin's system allows for both cladistic and phyletic evolution; whereas that of Eldredge and Gould appears 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 one or more phases of cladistic evolution (notably the cladogenesis of 2.3 million years B.P.) and other periods, possibly one earlier and most probably one later than that, of phyletic change (fig. 2). In this respect, the Darwinian pattern seems to be more versatile and to fit the facts of hominid palaeontology better.

(m) *Speciation and cladogenesis*

To my understanding of the views of Eldredge and Gould (1972), speciation requires a cladistic event to occur — so that one part of a species' range diverges from another part. They appear not to countenance the possibility that speciation can occur, through appropriate environmental change, without the splitting of a line. It would appear to me, from my study of hominid phylogeny, that speciation may occur with or without cladogenesis (the splitting of a lineage - Simpson, 1953; Rensch, 1959); but that cladogenesis cannot occur without speciation. As Simpson (1953, p. 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, p. 112) says 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 event, 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, 1974a, 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 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, pp. 353-354)

Julian Huxley was referring to such reticulate evolution especially in recent man. However, the very qualities of man, which Huxley believes have been and are responsible for his recent recombinational pattern of reticulate development, have almost certainly characterised 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 million years, 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 recognised 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 recognise its existence and its implications, since these run counter to the generally-accepted basis of taxonomic practice" (*op. cit.*, p. 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!

2. The Numbers of Early Hominid Individuals Recovered from African Sites (Table 2)

It would be dreary to recount the full tally of discoveries of fossil hominids in the recent past. Instead, I propose to give a brief resume of the material available at the present time. It is instructive to indicate the number of sites and specimens available in 1956, that is, shortly before the spate of East African fossil hominids began emerging. At that time, the overwhelming preponderance of African fossil hominids were from South Africa, while from East Africa only fragments representing at most five individuals had been recovered back in the 1930's. Thus, in 1956, only seven sites in Africa had yielded fossils of what are to-day generally regarded as early hominids. Five of these were in the Union of South Africa and these 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 (1948 onwards). These five South African sites had produced a good sample of fossil bones representing not fewer than 121 hominid individuals and possibly as many as 157 individuals. The two East African sites that had by 1956 yielded remains of early hominids were in the then Tanganyika, namely Olduvai and Garusi (now known as Laetoli), from which fragments ascribable to five individuals had been yielded. To take the middle value, bones representing some 144 early fossil hominid individuals were available from 7 African sites twenty-six years ago.

By to-day, as we commemorate the centenary of the death of Charles Darwin (on 19th April 1882) and as we assemble at the Pontifical Academy of Sciences in the Vatican a month later than the centenary, instead of 7

Table 2 — *African Sites of Early Hominids.*

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

we have 14 and perhaps 18 African sites. The number of sites in South Africa remains at five, but eight new East African names and one Saharan place-name have been added to the catalogues of African fossil hominid discovery-sites in just over a quarter of a century. The term 'site' hardly does 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; five new sites in Kenya are the Chemeron Beds and Chesowanja near Lake Baringo, Koobi Fora, Kanapoi and Lothagam near Lake Turkana (formerly Lake Rudolf); two new sites in Ethiopia, namely the Omo Valley in the south and Hadar in the north-east; and Yayo (Koro Toro) in the Chad Republic. The number of individuals represented by the 15 sites of South and East Africa has more than trebled. Instead of a minimum of 126 individuals, as in 1956, we have at our disposal an estimated minimum of 389 early hominid individuals and a possible maximum of 582 individuals, with a middle value of some 485 individuals (Table 3).

Two additional sites in the north of Kenya, Ngorora and Lukeino, have each yielded a hominoid molar tooth, the former an upper and the latter a lower, which are considered by some to have distinct hominid resemblances. On the other hand the hominoid remains from Lothagam and Kanapoi in northern Kenya may or may not have belonged to hominids. Thus Kenya's contribution to the early hominid listings comprises three sites certainly, with up to four possible additional sites.

To a human population biologist, for whom the sample size is often a critical consideration, 485 individuals is not a particularly large sample. This is especially true when one considers that these 485 individuals spanned no less than three million years, that is, from about four to about one million years before the present. If our fossils were evenly spaced in time — which of course they are not! — we should have one individual for every 6185½ years.

TABLE 3 — *25 Years of African Early Hominid Discoveries.*

1957	1982
From 7 Sites 121-157 Individuals Represented Mid-value 143	From 15 Sites 389-583 Individuals Represented Mid-value 485

Moreover, the stockpile of early hominid fossils falls into two different genera on most classificatory systems in use to-day (*Australopithecus* and *Homo*) and into different species, most commonly reckoned as four to seven in number, over the time period under consideration. Each species itself was dispersed in time and space, allowing of geographical and temporal variability, whilst, 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 woefully small.

Notwithstanding, accidents of preservation and the operation of taphonomic agencies have resulted in groupings of data into several fairly large sub-sets — such as the remarkable South African type collections of *A. africanus transvaalensis* from Sterkfontein and Makapansgat (comprising over 70 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 analyses have been made for the South African sites (Mann, 1968, 1975; Tobias, 1968a, 1974b) and for Olduvai (Tobias, 1982b) and some 225 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 preliminary accounts permit us to go at present.

Despite the shortcoming 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 nature of the morphological hominids and of the pattern of hominid evolution.

3. VARIOUS WAYS IN WHICH HOMINIDS MAY BE DEFINED

In a previous study (Tobias, 1975b), 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 palaeontologist, 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 sensori-motor 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 a 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 palaeo-anthropological record: for example, the possibility 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.

In this presentation I shall concentrate on the morphological picture and bring in brief reference to some of these behavioural traits.

4. 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-

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

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 Modification 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

vertebral alignment (fig. 4); (ii) development of structural mechanisms for the transmission of weight down the spinal column (fig. 5), 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 (fig. 6) 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.

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

(b) The re-deployment and restructuring of the upper limb, from an organ involved in weight-hearing, 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 (fig. 7), 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.

(d) Gross encephalization — the strong positively allometric enlargement of the whole brain and concomitantly of the capacity of the braincase (fig. 1).

(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.

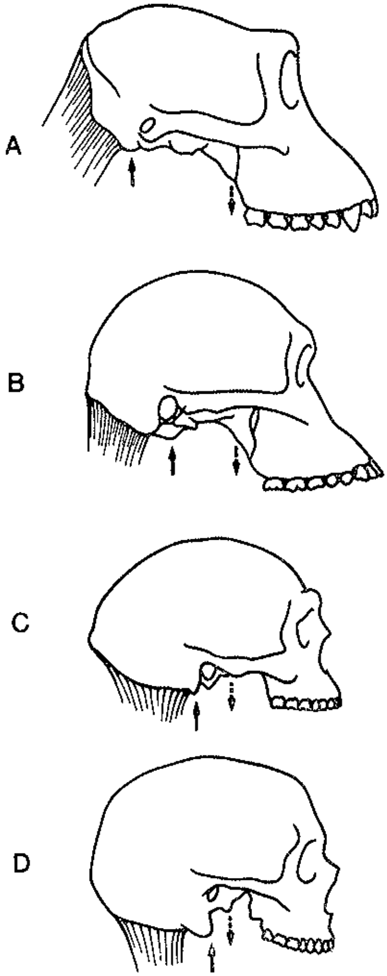


FIG. 4. Crania and restored nuchal muscles of four hominoids, A gorilla, B *Australopithecus africanus*, C *Homo erectus*, D *Homo sapiens*.
The downward-directed, broken arrow in each instance is the weight-line or line of centre of gravity of the cranium. The upward-directed, continuous arrow indicates the antero-posterior position of the occipital condyles through which the cranium articulates with the spinal column. With increasing grades of hominization the two arrows approximate each other. *Pari passu* with the better poise of the cranium on its condylar pivot, the bulk of the nuchal (back of neck) muscles is greatly reduced and the direction of their fibres becomes progressively more vertical.

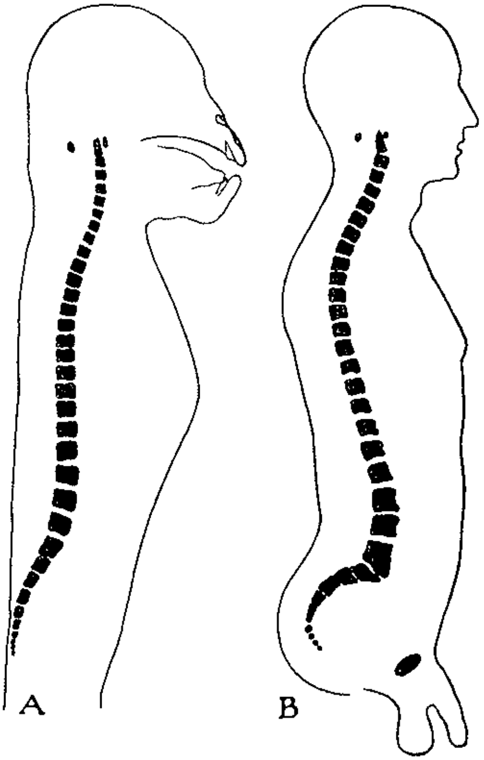


Fig. 5. Median sagittal sections through the head and trunk of a chimpanzee, A (after D.J. Cunningham, 1886) and of a man, B (after C.H. Stratz, 1905). The sections show the differences in the curvatures of the vertebral columns of ape and man, the cervical, lumbar and sacral curves being more marked in the upright human being. The sequence of vertebral body sizes from above downwards is another distinguishing feature: in upright man, the sizes increase more markedly towards the lower lumbar vertebrae, since each vertebra regularly supports a greater mass than the one above it.

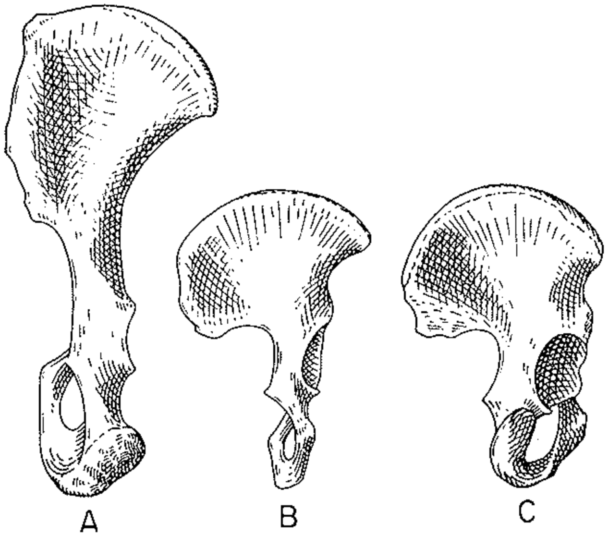


FIG. 6. Right ossa coxae (innominate bones) of chimpanzee (A), *Australopithecus africanus* (B) and modern man (C). In each instance, the bone is orientated with the plane of the ilium at right angles to the line of sight, and with the anterior superior iliac spine pointing to the viewer's right. The transversely expanded ilia of man and *Australopithecus* contrast with the narrow, vertically expanded ilium of the ape.

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

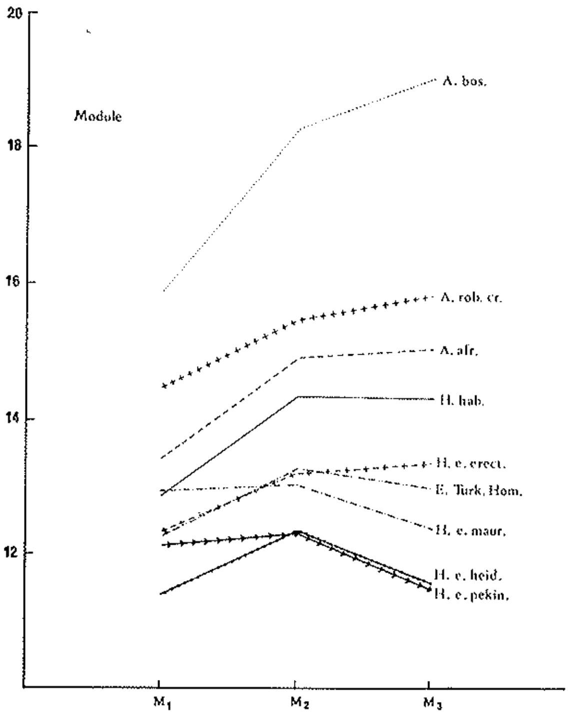


FIG. 7. To illustrate the overall size of the crown of a tooth, we may use the module which is 1/2 (mesiodistal diameter + buccolingual diameter). This diagram graphically depicts the mean modules of the three lower molars for each of a number of fossil samples. Tooth-size is shown thereby to diminish as one passes from *Australopithecus africanus*, through *Homo habilis*, to various populations of *Homo erectus*.

A. bos. = *Australopithecus boisei* (East Africa)
A. rob. cr. = *A. robustus crassidens* (Swartkrans)
A. afr. = *A. africanus transvaalensis* (Sterkfontein & Makapansgat)
H. hab. = *Homo habilis* (East Africa)
H. e. erect. = *H. erectus erectus* (Java)
E. Turk. Hom. = *Homo* from East Turkana (Kenya), probably a mixed sample comprising *H. habilis* and *H. erectus*
H. e. maur. = *H. erectus mauritanicus* (Morocco)
H. e. heid. = *H. erectus heidelbergensis* (Heidelberg, Germany)
H. e. pekin. = *H. erectus pekinensis* (Peking, China)

(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 (figs. 4, 8), (ii) the changes in size of the dentition and masticatory habit and vigour, and (iii) the enlargement and re-modelling of the 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 & b).

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 which blemishes are still with us despite the exponential increase in the treasury of fossils.

5. ENDOCRANIAL CASTS AS A GUIDE TO THE STUDY OF THE BRAIN

Like muscles, the brain leaves its mark upon bones. During embryonic, foetal and post-natal life, the form of the brain-case becomes accurately moulded over the surface of the expanding brain. The brain calls the tune in the determination of cranial form. The outside of the brain thus imprints itself upon the inside of the brain-case. In some areas even the convolutions or gyri, and the fissures or sulci that separate them, leave clear impressions on the interior of the calvaria. These *impressiones gyrorum*, in turn, give

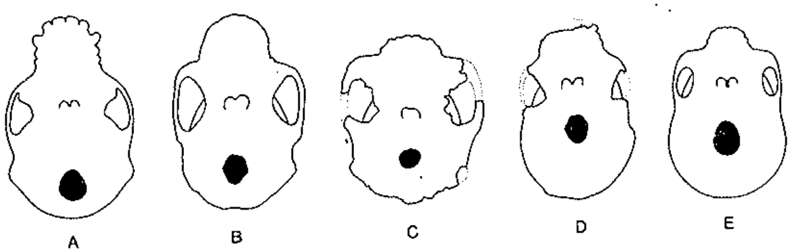


FIG. 8. One of the adjustments that accompanied the evolution of bipedalism was a progressively more anterior placement of the foramen magnum (shown black) and of the flanking occipital condyles, through which the skull articulates with the vertebral column.
Key: A - gorilla; B - *Australopithecus africanus* from Sterkfontein; C - *A. boisei* from Olduvai; D - *Homo habilis* from Olduvai; E - modern *H. sapiens*.

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

TABLE 8 (a) — *The Structural Basis of Speech.*

(a) CENTRAL — Expansion of Specific Central 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

character to an endocast, whether natural or artificial. Thus, with care, it may be possible for us to read off some of the markings that originally had bedizenned the surface of the brain.

Several studies have shown that the endocranial cast reproduces the form of the brain quite closely. In a comparison between endocranial casts and the corresponding brains, Connolly (1950) showed that fissural markings are clearly indicated in some parts of the endocasts, especially the lower regions. He found, too, that the impressions on the bone appear to become resorbed with old age. He concluded that the maximum degree of fissural marking on the skull, in hoth anthropoid apes and man, occurs probably in young adults. This is an advantage when applied to the fossil record, because a very large percentage of hominid bones available to us are of anatomically immature individuals. For example, out of some 160-170 South African ape-man specimens to which we can assign an individual age, 48 or 49% are immature and 51 or 52% are mature (Mann, 1968, 1975; Tobias, 1968a, 1974b). Thus, in a good percentage of our fossil individuals, death occurred at an age at which we can be reasonably sure that their skulls were well marked by brain fissures, if the situation in these early hominids was like that in modern apes and human heings.

Fissural markings are more likely to occur over certain areas of the cranium than over others. This was noted as long ago as 1907 by Gustav Schwalbe: he found that in modern man, the markings of the cerebral convolutions are appreciable on the basal aspect, the front and side-walls, but extend upwards for no more than one-third of the frontal bone. Above that the inner surface shows no relief. Weidenreich (1943) found the same distribution in the skulls of Peking Man (*Homo erectus pekinensis*) from Chou-K'ou-Tien, save that the junction between the area with strong relief and the smooth portion was higher up. At the junction between the well- and poorly-marked areas, there was a transverse line of swollen bone which Weidenreich, with his love of inventing names, called the *limen coronale*. Connolly (1950) likewise found this regional differentiation in the clarity of cerebral markings.

When I studied endocasts of the South African australopithecines, I was able to confirm that for this group, too, the markings were clear on the sides and base of the endocast, whereas the upper aspect was smooth and featureless (fig. 9).

These observations were perplexing, because the upper surface of the brain, in the fresh state, is just as full of character as the other parts! It occurred to me that gravity was the likely reason for this differential reflection of brain detail on the cranium. (I have recently found that Connolly had made the same suggestion in his 1950 book on "External Morphology of the Primate Brain"). It seemed to me that postural differences should be involved. If a creature walked upright, then for most of its life, the brain would exert maximum pressure on the base and side-walls, and little on the roof of the vault.

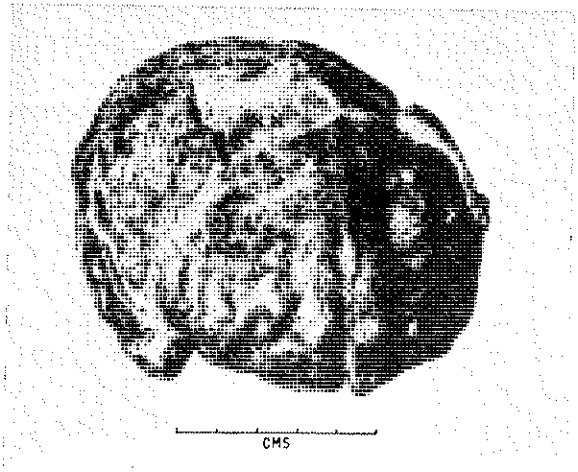


FIG. 9. An endocast of *A. africanus* from Sterkfontein. Note the well-marked *impressiones gyrorum* in the lower frontal lobe. X marks Weidenreich's *limen coronale*, the junction between well-fissured endocast below and smooth, poorly-marked endocast above. XX is the impression of a depressed fracture of the cranium.

I was excited by this line of thinking because at that time (I speak of the late forties), we were not yet sure if *Australopithecus* walked upright, like man, or in an obliquely quadrupedal fashion, as in apes. If my thinking were correct, an animal which was obviously quadrupedal should have good markings on the upper surface of its endocast as well, because with its head hanging down, there would be pressure on the forward-directed 'top' or dorsal aspect of the brain-case. I first noted such detail on the upper surface of a natural endocast of a quadruped in 1946; at that time, as a student under Professor R.A. Dart, I discovered and excavated an endocast and part of the cranium of a bovid (probably the small extinct *Bos makapani*), in the Buffalo Cave, near Makapansgat. This was during the early student expeditions I organised to Makapansgat which led, just over a year later, to the finding of the first *Australopithecus* cranium at Makapansgat.

On the same expedition, we discovered endocasts of another group of animals that did not walk upright. These were of baboons and monkeys and they came from the same layers (Members 3 and 4) of the Makapansgat cave deposit that subsequently yielded the ape-man. The beautiful convolutional detail on the upper surface of these endocasts was striking.

It seems that those areas of the interior of the cranium, which are, for most of the life of an animal, in a dependent position, show the best-preserved brain-markings.

With Connolly (1950), it must be stressed that the presence of a fissure or of a convolutional bulge on an endocast may yield valuable information, whereas the absence of an impression is of no morphological significance. For example, one of the deepest and most impressive fissures — the lateral or Sylvian fissure — usually leaves little mark upon the endocranium.

6. VARIATION IN THE VENOUS DRAINAGE OF THE BRAIN

The markings on the surface of the posterior parts of the endocasts permit one to infer the pathway followed by the drainage of blood in the system of cranial venous sinuses.

A. africanus of South Africa

In all seven of the *A. africanus* specimens from South Africa, where this region is preserved, the grooves on the endocranial surface (or the elevated impressions on the surface of the endocast) show that the venous sinus drainage followed the pattern which is modal in modern man. That is, the evidence shows that the superior sagittal sinus became continuous, across the confluence of the sinuses (*torcula Herophili*), with one or other of the transverse sinuses, usually the right.

A. robustus and *A. boisei*

An interesting variant, occasionally found in modern man, characterises the 'robust' australopithecines, *A. robustus crassidens* of Swartkrans and *A. boisei* of Olduvai and Koobi Fora ('East Rudolf'). This pattern was first detected by the author in the markings on the beautifully preserved occipital bone of the type specimen of *A. boisei*, namely Olduvai hominid 5 (Tobias, 1967, 1968b). It was found there that the sulcus for the superior sagittal sinus did not sweep around either to the right or to the left to form a transverse sinus sulcus. Instead, it continued downwards on the right side of the cruciate eminence, flowing directly into a large right *occipital sinus* groove. There was also a smaller left occipital sinus groove, which began as a depression on the left side of the inferior sagittal limb of the cruciate eminence. The occipital sinus sulci led into enlarged right and left *marginal sinus* grooves. These ran close to the margin of the foramen magnum, crossed the jugular process of the pars lateralis of the occipital bone and led directly to the jugular notch. It may be inferred that blood from the superior sagittal sinus flowed into the right occipital and right marginal sinus, whilst that from the inferior sagittal sinus and *sinus rectus* drained into a left occipital and left marginal sinus, so passing directly to the bulb of the internal jugular vein.

Each marginal sinus groove, as it approached the jugular notch, received an unusually narrow sigmoid sinus groove. Instead of the sigmoid sinus arising as the continuation of the corresponding transverse sinus, it was formed in *A. boisei* by the union of the superior petrosal sinus with a small petrosquamous sinus, close to the base of the petrous pyramid.

That is to say, the occipital-marginal sinus system had fulfilled the rôle usually played by the lateral sinus drainage system. In modern man, the blood-flow in the marginal and occipital sinuses (when these are present) is usually *towards* the confluence of the sinuses at the internal occipital protuberance. In *A. boisei*, this direction of flow must have been reversed, the blood following a seemingly shorter and more direct route to the bulb of the internal jugular vein.

A similar occipital-marginal drainage system was subsequently demonstrated by *Day et al.* (1976) in one other *A. boisei* cranium where this region is accessible, namely KNM-ER 407.

Meantime, the author has shown that this same interesting variant occurs in *A. robustus crassidens* as well: it is present in SK 46 and SK 859 (Tobias, 1968b) and in SK 1585 (according to Holloway, 1981a, though not mentioned nor depicted by him in his original description of SK 1585 - Holloway, 1972). Thus, it occurs in three out of three specimens of *A. robustus crassidens* in which the area is available for study. The only other Swartkrans cranium in which the area concerned is intact, namely SK 847, has the common lateral route (Tobias, 1968b); but whereas it was at first thought that this specimen was an *A. robustus crassidens* which lacked the unusual pattern, it was later shown to belong not to *A. robustus* but to early *Homo* (Clarke, Howell and Brain, 1970; Clarke and Howell, 1972; Clarke, 1977).

Homo habilis

In two Olduvai specimens assigned to *H. habilis*, OH 13 and OH 16, the region in question is sufficiently well-preserved to reveal that the common lateral drainage route was followed, as in *A. africanus* and in modern man.

The Hadar specimens

These specimens — which have been assigned to a proposed new species *A. afarensis* Johanson, White and Coppens 1978 — include two crania that preserve the critical region. It is of interest to note that Holloway (1981a) reports that "the adult cranium from Hadar and the infant AL-333-45 (Johanson and White, 1979) *also* have a clear impression of the accessory (sic) occipital and marginal sinus, and although named *A. afarensis*, the morphology to this author's mind is more reminiscent of a smaller robust Australopithecine" (*op. cit.*, p. 117). Holloway's remarks about the possibly 'robust' affinities of these two Hadar specimens are interesting in the light of the fact that Johanson and Taieb (1976, p. 297), in their preliminary account of the Hadar fossils, thought they could detect the presence of three synchronic and sympatric taxa: "On the basis of the present hominid collection from Hadar it is tentatively suggested that some specimens show affinities with *A. robustus*, some with *A. africanus* (*sensu stricto*), and others with fossils previously referred to *Homo*". Subsequently, Johanson *et al.* (1976) narrowed their identification of the Hadar fossils into 'two clear groups', namely, 'something resembling but most probably more primitive than *A. africanus*' and 'the presumed *Homo* group'. Even then, however, although they no longer spoke of the third group (c.f. *A. robustus*) at Hadar, they again drew attention to robust elements in certain of the Hadar fossils (*op cit.*, pp. 128-129):

> "... it is possible that A.L. 211-1 and A.L. 166-9 may represent an early occurrence of a robust australopithecine lineage. The somewhat atypically robust character of the temporal may be considered as consistent with the idea that the early stages of the robust lineage are being sampled".

However, little mention is made of the supposed robust elements at Hadar in the more recent writings of these authors (e.g. White, Johanson and Kimbel, 1981), although they have now been at pains to demonstrate supposed robust elements in the South African fossils of *A. africanus*! Holloway's reference to the occipital-marginal venous sinus drainage occurring in what are apparently the only two Hadar specimens in which the appropriate area is preserved revives the originally mooted possibility that 'robust' elements *are* indeed present in the Hadar population, whatever the taxonomic significance of these elements may be.

Holloway (1981a) has, on the other hand, used the *absence* of 'accessory occipital and marginal sinuses' from the Omo L338y-6 cranium (which Rak and Howell, 1978, had identified as a juvenile *A. boisei*) to support his reticence in accepting that the Omo specimen belongs to *A. boisei*. However, it would at this stage perhaps be imprudent to consider the absence of enlarged occipital-marginal sinuses, and the three other encephalic features cited by Holloway (*op. cit.*, pp. 115-116), as outweighing all the other cranial morphological evidence adduced by Rak and Howell (1978) in favour of the identification of the Omo cranium as that of an *A. boisei* child.

If we continue to regard Omo L338y-6 as an *A. boisei* child (*pace* Holloway), it would mean that the incidence of occipital-marginal sinus drainage in the *A. boisei* group is 2 out of 3 individuals, in *A. robustus crassidens* 3 out of 3, in Hadar hominids 2 out of 2, in *A. africanus* 0 out of 7 and in *H. habilis* 0 out of 2. The figures for drainage of the superior sagittal sinus groove into the occipital-marginal sinus grooves in modern man are 1 out of 44 (Knott, 1882), 2 out of 100 (Woodhall, 1936, 1939), 3 out of 216 (Petriková, 1963) and 3 out of 210 (Tobias, 1968b); while in modern apes the incidence found by the author was 0 out of 31 in chimpanzee and 0 out of 23 in gorilla (Tobias, 1968b).

The robust and hyper-robust australopithecines, as well as the Hadar hominids, seem to be characterised largely by the retention of the infantile arrangement of direct drainage through the occipital-marginal route; whereas *A. africanus*, *H. habilis* and modern man are marked by the more circuitous, trans-cerebellar route of the transverse and sigmoid sinuses.

7. Endocranial Capacity of Early Hominids

In modern Primates evidence as to the size of the brain is furnished by volumetric or gravimetric studies on actual brains, or by the capacity of the calvaria. In ancient forms, one is dependent upon either the volume of endocranial casts or the capacity of calvariae. Such studies have revealed that, while the increase in brain-size was one of the most dramatic and sustained elements in the complex of hominizing changes, it was scarcely evident in *Australopithecus* (figs. 1, 10).

In absolute size, the mean cranial capacity of *A. africanus* was about

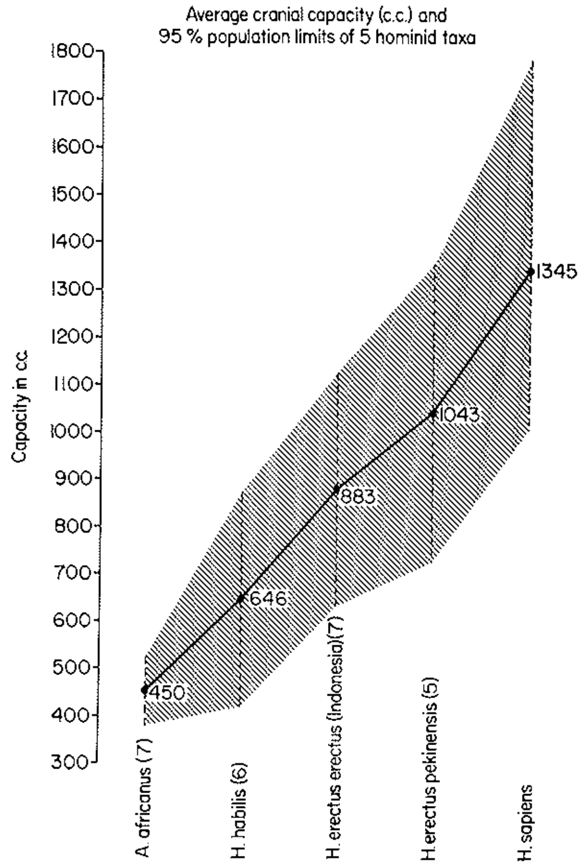


Fig. 10. Mean cranial capacity and 95% population limits of each of five fossil hominid samples. The chart reveals the dramatic trebling of absolute cranial capacity of hominids in about three million years.

450 cc. This average is 1.2 times the mean in chimpanzee, 1.1 times that for orang-utan and 0.9 of the mean in gorilla. In a word, this kind of creature was no brigger-brained, in absolute terms, than the extant great apes of Africa and Asia. Indeed this was a cardinal reason why, for decennia, the world was reluctant to accept *A. africanus* as a member of the Hominidae.

Of course brain-size must bear some relationship to body size. The French comparative anatomist, Cuvier, first introduced the concept of relative brain weight, that is, the weight of the brain expressed as a fraction of the weight of the body. Several studies since then have shown that, within the human species, brain-size does not vary with body weight (as Matiegka, 1902 and Pearl, 1905, had believed), but with body stature (Pakkenberg and Voigt, 1964; Spann and Dustmann, 1965; Schreider, 1966; Tobias, 1970, 1971a, 1971b, 1975a). The correlation coefficient between brain weight and body height is a moderate positive one, 0.26 in males and 0.31 in females (Schreider, 1966). This applies within the species *Homo sapiens*. Does it apply when we compare different species?

A series of studies by Snell (1891), Dubois (1897), Bauchot and Stephan (1964-1969) and Thenius (1969) have shown that, when we compare closely related species, there is a linear relationship between brain weight and body weight on a double logarithmic scale. A species in which the members are on average heavier will be expected to have a larger average brain-size than one with lighter bodies. This fits the relationship between *A. africanus*, on the one hand, and *A. robustus* and *A. boisei* on the other: in the latter groups the mean brain-size was about 504 cc or 12 per cent larger than in the former. The evidence of the postcranial bones indicates that, although the two groups do not seem to have been of appreciably different stature, robust australopithecines must have been of heavier body build than *A. africanus* of the Transvaal and Hadar. The small increase in brain size represents no more than one would expect from the general increase in body bulk: the expansion of the brain from earlier *A. africanus* specimens to the later robust australopithecine fossils seems to have been only slightly allometric.

It has been mentioned that the brain-size of *A. africanus*, in absolute terms, was not greater than that of modern anthropoid apes. It is of course possible that the body size of *A. africanus* was smaller than that of the extant apes: in this event the presence of ape-sized brains in the smaller-bodied australopithecines should be of some significance — it would connote that the brain-size of *Australopithecus* could well have been *relatively* slightly larger than that of modern apes.

However, the notable hominid trend towards and of markedly allometric brain enlargement, absolute and relative, is not detectable at the stage of *Australopithecus*. Appreciable absolute and relative brain enlargement came later, with the advent of the genus *Homo* (Tobias, 1971a, 1980). This occurred along the other lineage derived from *A. africanus*, that is, the line of the genus *Homo* leading to modern man. The earliest species along that lineage was recognised by the late L.S.B. Leakey, Napier and myself (1964) in the 1.8 million-year-old fossils from Olduvai, to which we gave the name *Homo habilis.*

Four crania of *H. habilis* from Olduvai Gorge, in northern Tanzania, have permitted estimates to be made of their respective capacities (fig. 11). Three of these are of immature individuals and one is sub-adult: it has therefore been necessary to compute 'adult values' for three of these specimens. The latest values obtained for these four Olduvai crania, superseding those published by myself earlier, are as follows:

	Estimated total capacity	Estimated 'adult value'
Olduvai hominid 7	647 cm^3	674 cm^3
Olduvai hominid 13	660 cm^3	673 cm^3
Olduvai hominid 16	622 cm^3	638 cm^3
Olduvai hominid 24	597 cm^3	597 cm^3

The varying adjustments from the estimated total capacity to the estimated 'adult value' are based on the varying degrees of immaturity of the four specimens, OH 7 being the youngest and OH 24 the oldest.

Two determinations for East Turkana specimens that the author considers belong in the same taxon (*H. habilis*) are available: they are 770-775 cm^3 for KNM-ER 1470 (Holloway, quoted by Day *et al.*, 1975 and by Leakey, Leakey and Behrensmeyer, 1978) and 505-510 cm^3 for KNM-ER 1813 (Holloway, quoted by Day *et al.*, 1976 and by Leakey, Leakey and Behrensmeyer, 1978). KNM-ER 1470 belongs to an adult individual and therefore no age adjustment to its capacity is necessary. KNM-ER 1813 must be adjudged sub-adult; its unworn third molar crowns "still face a little buccally and distally, indicating incomplete eruption" (Day *et al.*, 1976, p. 393). On this basis, its capacity probably is about 99 per cent of adult size (i.e. between the 98 per cent of OH 13 and the 100 per cent of OH 24). If we take 507.5 cm^3, the mid-value of Holloway's range, it would give an 'adult value' of 512.6 cm^3 or a rounded off value of 513 cm^3. The extremes of Holloway's range of estimates (505-510 cm^3) yield 'adult values' of 510 cm^3 and 515 cm^3 respectively. If those two specimens do indeed belong to the same taxon as the four from Olduvai — and dental and other morphological evidence points strongly in this direction — they considerably widen the sample range and the variability of cranial capacity in *H. habilis.*

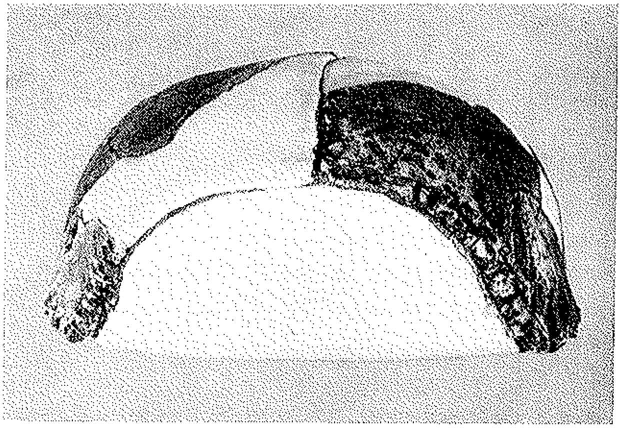


FIG. 11. The partial endocranial cast in position beneath the two parietal bones of Olduvai hominid 7, the type specimen of *Homo habilis*.

The sample of 6 *H. habilis* crania thus has 'adult values' of 513, 597, 638, 673, 674, 770-775 cm^3, or a mean of 645 cm^3. The three putative males (OH 7, OH 16 and KNM-ER 1470) have a mean of 695 cm^3 and the three putative females (OH 13, OH 24 and KNM-ER 1813) one of 594 cm^3. The index of sexual dimorphism based on these minute samples is 14.5 per cent (of the putative male mean) and 17.0 per cent (of the putative female mean). Such degrees of sexual dimorphism are encountered in modern orang-utan and gorilla and have been found in 8 out of 67 modern human cranial series (Tobias, 1975a).

The East African *H. habilis* sample mean of 645 cm^3 represents an increment of 195 cm^3 or 43.3 per cent on the mean for *A. africanus*. This remarkable increase in hominid brain-size is first apparent in the fossil record about 1.8 million years B.P. It must have occurred some time between about 2.5 million and 2.0 million years ago. The trend was to continue for more than another million years, until the modern human trait of brain-size about three times that of modern apes (in absolute terms) was attained.

Of the Laetoli and Hadar hominids that have been assigned to the supposed new species *A. afarensis*, White *et al.* (1981) report that Holloway has obtained an approximate cranial capacity of 500 cm^3 for A.L. 333-45. This is described as an infant cranium, so its 'adult value' would be greater than 500 cm^3. Such a value would place it within the sample range of the robust australopithecine cranial capacities with mean of

504 cm^3, and it would probably have fallen outside the 95 per cent populations limits estimated for *A. africanus* (390.8-491.6 cm^3 - Tobias, 1975a).

For one other Hadar cranium, A.L. 162-28, White *et al.* (1981) state that an estimate of its cranial capacity is not yet available, but "this cranium is significantly smaller than any known *A. africanus* specimen" (*op. cit.*, p. 456, foot-note).

Of all the hominizing trends we have so far reviewed, the onset of excessive brain-size enlargement seems to have been most closely related in time to the appearance of stone tools made to a consistent pattern in durable materials.

We see two striking contrasts between *A. africanus* and *H. habilis*: *Australopithecus* is not associated with implemental activities in hard and imperishable materials and his brain-size is absolutely no bigger than that of the modern apes. *Homo habilis* is associated with stone tool manufacture and his brain-size is nearly half as great again as that of *Australopithecus africanus* and those of the extant Asian and African pongids. The inception of these two trends is remarkably coincident in the hominid record. Since the brain in general is the seat and controlling centre of function and behaviour, this is not an entirely surprising association.

8. Two Patterns of Encephalic Increase in Early Hominids

The increased brain-size from *A. africanus* to *A. robustus*/*A. boisei* is different in several respects from the increase manifest in *Homo habilis*. We have seen that the augmentation, on admittedly small samples, is about 12 per cent in the robust australopithecines, but 43 per cent in *Homo habilis*. The other major difference is that in the robust lineage, there are no indications of further progressive reorganisation, whereas in the *Homo* lineage, beginning with *H. habilis*, there are signs of such reorganisation beyond the australopithecine grade. The robust offshoots had bigger cheek teeth, robuster bones, sturdier muscles and a heavier body; while *H. habilis* had smaller teeth, probably gracile bones, slender muscles and a light body. Thus while brain enlargement in the robust ape-men is only slightly allometric, in *H. habilis* it is markedly positively allometric (Pilbeam and Gould, 1974).

At this level of hominid phylogeny, the changes marking the inception of early *Homo* are predominantly cerebral and, as we shall see, cultural-behavioural, and only minimally dental and gnathic. On the other hand, the changes marking the initial kick on the robust line are predominantly dental and gnathic, but only minimally cerebral and cultural-behavioural. Hence, the divergence of *Australopithecus* into two different lineages is effected by markedly disparate kinds of mosaic development. In one, the evolution of the brain is not obtrusively involved; in the other, it plays an all-important rôle.

9. DIFFERENTIAL BRAIN DEVELOPMENT

Brain-size as a whole is a crude measure of encephalization. However, a close study of the endocranial casts of the early hominids shows that differential enlargement was a striking feature, probably of considerable functional significance.

One set of regional differences resides in the area of the inferior frontal convolution. The posterior part of this gyrus is unexpanded and unremarkable in the brains of apes, but is full and rounded in modern man, where it is known as Broca's area. This is one of the seats of speech in the brain. The corresponding area in the endocast of *Australopithecus africanus* (as Schepers, 1946, long ago pointed out) is well developed, as it is in the endocasts of *Homo habilis* and *H. erectus*. It would seem then that part of the cerebral basis of the speech mechanism had appeared in the earliest hominids of the genus *Australopithecus*.

Another set of regional differences is located in the parietal lobe.

In Dart's first paper on the Taung child, the type specimen of *Australopithecus africanus*, he focussed attention upon the parietal lobe and the lunate sulcus in the beautifully preserved natural endocast of that pioneering discovery. He stated: "...the *sulcus lunatus* has been thrust backwards towards the occipital pole by a pronounced general bulging of the parieto-temporo-occipital association areas" (Dart, 1925, pp. 197-198). Dart was supported in his identification of the lunate sulcus by Schepers (1946) and by Holloway (1975) who speaks of this posterior placement of the lunate sulcus of the Taung child's endocast as "perhaps the most conclusive proof for reorganisation of the brain from a pongid to human pattern" (*op. cit.*, p. 404). Holloway adduced indirect evidence that the lunate sulcus on a robust australopithecine endocast (SK 1585) he described from Swartkrans must have been in a similar posterior position (1972). Dart's placement of the lunate sulcus has not gone without challenge. Keith (1931) identified the lunate sulcus as probably lying further forward on the brain-cast and not in the position indicated by Dart. In this more anterior position it would not differ in location from that of modern apes' brains. Le Gros Clark (1964) was more cautious when he stated that it is really not possible to identify the lunate sulcus with certainty from the impressions on the australopithecine endocasts, a view with which the present author finds himself in agreement. Weidenreich (1936) said the same about the endocasts of *H. erectus pekinensis* and von Bonin (1963) about that of *H. erectus erectus* I.

Thus until lately, Holloway was the only recent staunch upholder of Dart's claimed position of the lunate sulcus in the Taung endocast. In a recent exchange with Falk (1980a, 1980b), Holloway has re-examined the question and appears to have diluted the assurance of his original identification of the lunate sulcus of Taung. He now states: "*We cannot prove where the lunate sulcus is located, but only demonstrate where it is not*". (Holloway's emphasis) (Holloway, 1981b, p. 49). Further on we find Holloway declaring: "*It is thus possible that the Taung specimen has no typical lunate sulcus to observe*". (Holloway's emphasis) (*op. cit.*, p. 50).

However, the supposed or actual placement of the lunate sulcus on the surface of the cerebrum does not provide the only possible evidence of the expansion of the parietal lobe. Dart (1925) drew attention to the rounded fullness of the parietal region and this is apparent, too, in endocasts from Sterkfontein (Schepers, 1946). The expansion affects especially the upper part of the region of the parietal lobe, the area occupied by the superior parietal lobule. This lobule is the region close to the medial border of the hrain and it intervenes between the postcentral gyrus and the parieto-occipital sulcus behind. The superior parietal lobule is clearly expanded in the brain of modern man as compared with that of apes (Bailey, von Bonin and McCulloch, 1950; Connolly, 1950); such expansion is apparent already in the endocasts of the earliest hominids.

The lower part of the parietal lobe — the inferior parietal lobule — is a most distinctive region of the human brain. Indeed of this lobule the claim has been made that it represents the only 'entirely new structure' to have appeared in the evolution of the human brain (Geschwind, 1965). The lobule comprises in the main two gyri, the supramarginal gyrus about the upturned end of the lateral or Sylvian fissure, and the angular gyrus about the upturned posterior end of the superior temporal sulcus.

This interesting area of the brain is characterised by rather special features. The arrangement of the gyri is highly variable. The area is late to myelinate (it is one of Flechsig's 'terminal zones'). Its dendrites appear very late and the cellular maturation of the lobule is delayed and may occur only in late childhood. It receives few afferent fibres from the thalamus. Phylogenetically it is a new region of the cortex. It is not concentric about one of the primary projection areas for vision, hearing or tactual sensibility, but lies at the point of junction of the primary projection areas for these three modalities; above and below it is flanked by attenuated or squeezed-out areas of cortex that Elliot Smith (1907) called the visuo-sensory band and the visuo-auditory band respectively. It appears to function as an *association area of association areas*, or a *secondary association area* in more classical parlance (Geschwind, 1965, pp. 273-275).

No trace of this inferior lobule is detectable in the macaque. It is present, though only in rudimentary form, in apes (Critchley, 1953; Geschwind, 1965; Bailey, von Bonin and McCulloch, 1950; c.f. Connolly, 1950). Geschwind (1965, p. 276) acknowledges that "the exact degree of the uniqueness of the inferior parietal region in man remains to be determined".

Sited between the areas of three great sensory modes — seeing, hearing and feeling — the inferior parietal lobule probably is involved in cross-modal associations. For this and further reasons, Geschwind and others believe that the region is involved in the development of speech, since cross-modal associations are a prerequisite to the ability to acquire speech. Indeed the second major 'speech centre' of the human brain, Wernicke's area, includes the inferior parietal lobule, as well as the superior temporal gyrus and the planum temporale on the upper surface of the temporal lobe.

This region in the fossil endocasts is not well-preserved, for the Sylvian fissure is notoriously 'silent' in declaring its presence by markings on the endocranial surface. Hence it is usually not possible to detect whether asymmetry of the length and of the posterior termination (the 'Sylvian point') of the Sylvian fissure was present in an endocast. What can be detected, however, is the rounded fullness of the region in the endocasts of later hominids including modern man. When we explore this region on the ancient hominid endocasts, however, we find that in the australopithecines the area which one would expect to be occupied by the inferior parietal lobule is not well-rounded; indeed it is commonly flattened or even depressed, in comparison with the well-rounded contour of the superior parietal lobule above. On the other hand, the endocast of *Homo habilis* shows a full elevation in this region of the inferior parietal lobule.

The evidence suggests that only part of the cerebral basis for speech was present in *Australopithecus* (Broca's area), whereas in the larger endocasts of *H. habilis* there is evidence of both Broca's and Wernicke's areas. (A third speech centre, the supplementary motor area, MsII, lies on the medial surface of the frontal lobe of the cerebral hemisphere: since this surface does not impinge upon the endocranium, its presence cannot be detected on an endocast too).

The endocasts thus provide evidence that the neurological basis of speech, as far as it can be detected on an endocast, was present in part only in *Australopithecus*, whereas both Broca's and Wernicke's areas seem to have been well developed in the brain of *H. habilis*.

The presence of the neurological basis of speech on the brain does not mean that *H. habilis* was necessarily capable of speech; but it is at least strongly suggestive that the parts of the brain that govern spoken communication were present from that stage where (a) brain enlargement became obtrusive, and (b) tools of hard materials appeared in the record.

10. THE AIRWAY AND SPEECH

Like other skilled human activities, speech depends upon a peripheral structure-function complex as well as a central nervous control system. Since it has been proposed recently that the peripheral structure of the pharynx and larynx, as inferred from the basis cranii, imposed severe limitations on the possibilities of speech in Neandertal man, it would be well for us to examine some of the evidence. The capability of making speech sounds peripherally appears to depend on the development of a nasopharynx and the 'descent' of the larynx (fig. 12).

At what point in the primates do we first find the appearance of a recognisable nasopharynx? It is clearly not present in lower Primates. In the *Tupaia* or tree shrew, the primate status of which is uncertain, the epiglottis rises up to make snug contact with the posteriorly elongated soft palate, while the laryngeal aditus faces slightly forwards, not backwards as in man. Thus there is continuity between nasal chambers and larynx. This makes for a complete airway and the animal cannot do other than breathe through its nose. Negus (1965) has shown that the continuity of the airway, by close nesting of the epiglottis against the soft palate, is most striking in animals which are *macrosmatic* (that is, whose way of life depends heavily upon smell), and in which the smell-organ and smell-brain are highly developed.

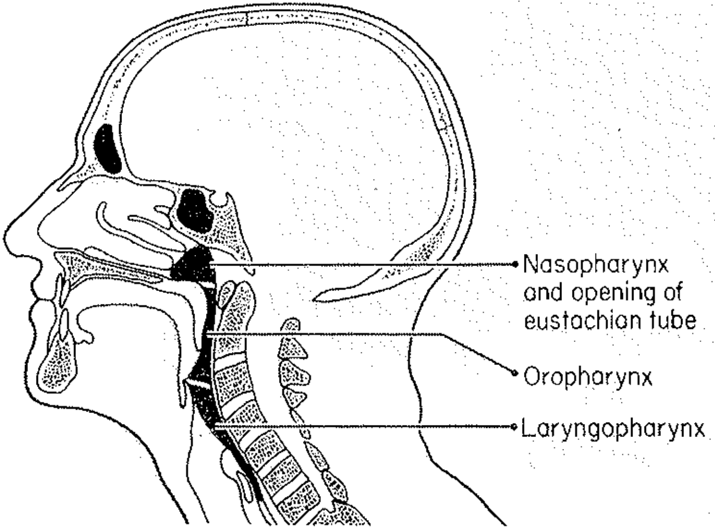


FIG. 12. Median sagittal section through the head of a modern man. The three subdivisions of the pharynx are clearly shown.

As one ascends through the primate scale, one finds several changes occurring (fig. 13). The intimacy of contact between epiglottis and soft palate is gradually lost; the laryngeal aditus comes to face at first upwards and then in increasing degree posteriorly; a continuous foodway between the mouth and oropharynx becomes established, so interrupting the continuity between nasal cavities and larynx.

For example, in the monkey, the epiglottis just meets the soft palate and there is a small interruption between the airway of the nose and of the larynx. The laryngeal aditus faces upwards and backwards.

By the stage of the lesser apes, the gibbons and siamangs, the epiglottis stops short of the soft palate, and there is a clear interruption between the nasal chamber and the larynx. Here, for the first time, say Wood Jones (1940) and DuBrul (1958), we may speak of a nasopharynx.

The 'descent' of the larynx continues through the great apes, the chimpanzee and gorilla of Africa and the orang-utan of Asia, and the gap between the epiglottis and the soft palate increases (fig. 13). So too does the interruption of the airway between the nasopharynx and the larynx. Hence, it is now possible in these apes, as in man, for air to come through the mouth as well as through the nose.

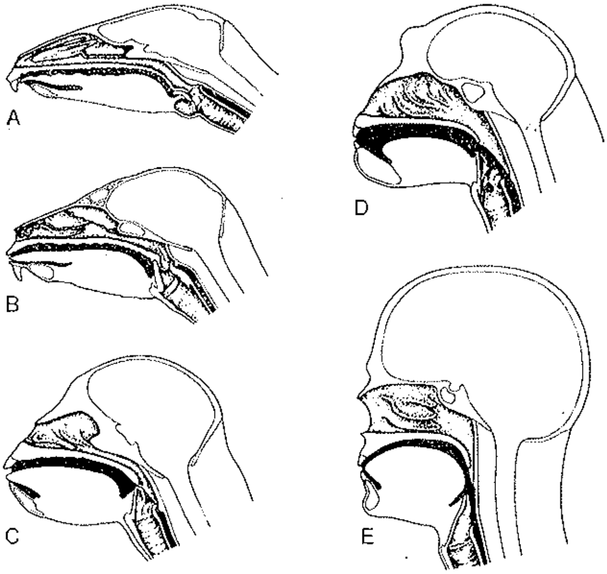


FIG. 13. Morphological grades in the upper respiratory tract or airway (stippled) and in the upper alimentary tract or foodway (black), to show the appearance of the nasopharynx, the disengagement of uvula and epiglottis, and the 'descent' of the larynx. A "vocal tract" emerges in the great apes and man.
A tree-shrew; B lemur; C monkey; D chimpanzee; E man.
(Re-drawn after DuBrul, 1958, and Negus, 1965)

This process reaches its extreme degree of development in modern man, while in earlier kinds of hominids the evidence suggests that intermediate degrees of development between those of the living great apes and of modern man must have existed.

In sum, we may say, with DuBrul (1958), that a nasopharynx as such came into being relatively late in the evolutionary story and only at a high point in the development of our Primate order of mammals.

It is interesting to note that the possibility of an airstream through the mouth becomes most highly developed at that level in the Primates where speech becomes possible. Thus, man, the speaking primate, has a mechanism by which he has a remarkably free airway through the mouth as well as through the nose (DuBrul, 1972, 1974). A considerable number of our speech sounds, vowels as well as consonants, are formed by the ejection of the airstream through the lower pathway, the mouth. If we had not that separation between the epiglottis and soft palate, speech as we know it in modern man would not have been possible. As a corollary, it may be noted that, since in the apes there is a separation between epiglottis and soft palate, apes have the peripheral anatomical potential to make some speech sounds even though they do not speak. As early as 1916, Furness reported that he had been able to teach an orang-utan to say *papa* and *cup*, while Hayes and Hayes (1951, 1952) where able to teach a young female chimpanzee, Viki, to pronounce four words — *mama*, *papa*, *cup* and *up* — though they were "pronounced with a heavy chimpanzee accent" (Fouts, 1975). After the Gardners' (1969) success in teaching the chimpanzee Washoe to communicate by American Sign Language for the Deaf, and the Premacks' (1971, 1972) study of chimpanzee Sarah's acquisition of language skills by the use of coloured pieces of plastic as words, Allan and Beatrice Gardner have turned their attention from language to speech and are reported to be training an ape to speak. So it would seem that there is a peripheral anatomical capacity for an ape to make some speech sounds, though it must be severely limited by the highly attached ape tongue, compared with the freely mobile tongue of man. Lieberman (1975) has stressed that the particular form that human spoken language has taken appears to be the result of the evolution of the modern human supralaryngeal vocal apparatus, an anatomical nuance that he feels was absent from such earlier hominids as the australopithecines and even from so recent a human race as Neandertal man. There is some difference of opinion as to how valid are the reconstruction of the vocal tract from fossil remains, and the inferences drawn therefrom on the capacity for speech; doubts have been expressed, too, about the assumption that one may draw valid conclusions about the capacity for speech and about the nature of a spoken language from the anatomy of the vocal tract, as dissected in extant hominids or reconstructed in extinct ones.

The important point is that even apes show the presence of a nasopharynx, the structural capacity for an airstream through the mouth and 'descent' of the larynx — the morphological prerequisites for vocalization. It is hardly to be expected that these features were less in evidence in *Australopithecus*, while in *H. habilis* and more advanced members of the hominine lineage they must have been even nearer to the modern human condition.

It would be a reasonable inference that the peripheral structure of the airway and the pharynx were such as to have permitted a number of speech sounds to have been made even by *H. habilis*, probably more than in the apes and in *Australopithecus*, though less than in *H. sapiens*.

It is suggested then that *H. habilis* had both the neural basis and the peripheral capacity for speech.

11. Speech and Culture

The humanness of speech was commemorated close on 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 that 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 tool-making ability and that he was responsible for those cultural assemblages designated Oldowan (M.D. Leakey, 1971). This lithic cultural phase was characterised by a predominance of tools known as choppers, while other forms recognised 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.*, p. 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 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 palaeontological 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 the 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.*, p. 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 organisation. Such operations characterise pre-operational intelligence, the second of Piaget's three major stages in the ontogenetic sequence of intelligence he recognises (sensori-motor 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 palaeoethology 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 a 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? (fig. 14).

12. CONCLUSION

It is postulated here that:

(a) *H. habilis* had the anatomical structure, both cerebral and vocal, which made speech possible;

(b) *H. habilis* possessed a culture which was of an advanced degree of complexity and embraced concepts beyond those attained by living pongids;

(c) this culture was of an order of complexity and reflected a level

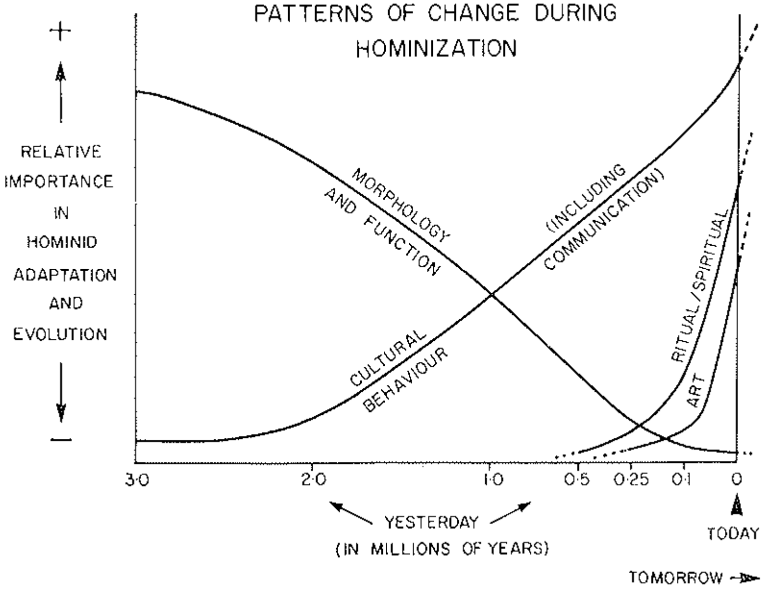


FIG. 14. The relative importance in hominid adaptation and evolution, of certain broad modalities of change, between 3 million years ago and the present.

of intelligence that virtually demanded speech for the transmission of the culture to the young;

(d) that the culture of *H. habilis*, adapting and evolving, was indeed transmitted to the young over hundreds of thousands of years, by such a means that cultural advances and innovations, too, were handed on to the young;

(e) that this activity — which the genetic heritage made possible — was handed on by social transmission;

(f) that speech is the most effective mechanism for cultural transmission that has yet appeared on earth;

(g) that *H. habilis*, in short, was a hominid capable of speech, albeit rudimentary 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 am deeply indebted to the Pontifical Academy of Sciences, and its President, Professor Carlos Chagas, for inviting me to participate in the Working Group on "Recent Advances in our Knowledge of the Evolution of Primates".

My thanks are due to Christel Eckert, Clare Huxley, Colin Richards, Peter Faugust and countless others who have helped and stimulated my researches on our African ancestors over the past 37 years.

REFERENCES

ABEL O., *Paläobiologie und Stammesgeschichte*. Jena: Fischer (1929).

AGER D.V., *The Nature of the Stratigraphic Record*. New York: John Wiley (1973).

BAILEY P., BONIN G. VON and MCCULLOCH W.S., *The Isocortex of the Chimpanzee*. Urbana: Univ. of Illinois Press., pp. 1-440 (1950).

BAUCHOT R. and STEPHAN H., *Le poids encéphalique chez les Insectivores Malgaches*. « Acta Zool. », *45*, 63-75 (1964).

BAUCHOT R. and STEPHAN H., *Hirn-Körpergewichtsbeziehungen bei den Halbaffen (Prosimii)*. « Acta Zool. », *46*, 209-231 (1965).

BAUCHOT R. and STEPHAN H., *Données nouvelles sur l'encéphalisation des Insectivores et des Prosimiens*. « Mammalia », *30*, 160-196 (1966).

BAUCHOT R. and STEPHAN H., *Encéphales et moulages endocraniens de quelques insectivores et primates actuels. Problèmes actuels de Paléontologie*. « Coll. Internat. C.N.R.S. », *163*, 575-586 (1967).

BAUCHOT R. and STEPHAN H., *Étude des modifications encéphaliques observées chez les Insectivores adaptés à la recherche de nourriture en milieu aquatique*. « Mammalia », *32*, 228-275 (1968).

BAUCHOT R. and STEPHAN H., *Encéphalisation et niveau évolutif chez les simiens*. « Mammalia », *33*, 225-275 (1969).

BONIN G. VON, *The Evolution of the Human Brain*. Chicago: University of Chicago Press, 1-92 (1963).

BOOKSTEIN F.L., GINGERICH P.D. and KLUGE A.G., *Hierarchical linear modeling of the tempo and mode of evolution*. « Paleobiology », *4*, 120-134 (1978).

BRACE C.L., *Krapina, "Classic" Neanderthals, and the evolution of the European face*. « J. Hum. Evol. », *8*, 527-550 (1979).

BRACE C.L., *Tales of the phylogenetic woods: the evolution and significance of evolutionary trees*. « Am. J. Phys. Anthrop. », *56*, 411-429 (1981).

BRAINERD C.J., *Recapitulationism, Piaget, and the evolution of intelligence; déjà vu*. « The Behavioral and Brain Sciences », 2, 381-382 (1979).

BROOM R., *The Pleistocene anthropoid apes of South Africa*. « Nature », *142*, 377-379 (1938).

CLARK W.E. LE GROS, *The Fossil Evidence for Human Evolution*. (2nd edn), Chicago: University Press (1964).

CLARKE R.J., *The cranium of the Swartkrans hominid SK 847 and its relevance to human origins*. PhD thesis. University of the Witwatersrand (1977).

CLARKE R.J. and HOWELL F.C., *Affinities of the Swartkrans 847 hominid cranium*. « Am. J. Phys. Anthrop. », *37*, 319-336 (1972).

CLARKE R.J., HOWELL F.C. and BRAIN C.K., *More evidence of an advanced hominid at Swartkrans*. « Nature », *225*, 1219-1222 (1970).

CONNOLLY C.J., *External Morphology of the Primate Brain*. Springfield, Ill.: Thomas, 1-378 (1950).

COPPENS Y., *Le cerveau des hommes fossiles*. « C.R. Acad. Sci. », 3-24 (1981).

CRITCHLEY M., *The Parietal Lobes*. London (1953).

CRONIN J.E., BOAZ N.T., STRINGER C.B. and RAK Y., *Tempo and mode in hominid evolution*. « Nature », *292*, 113-122 (1981).

DART R.A., Australopithecus africanus, *the man-ape of South Africa.* « Nature », *115*, 195-199 (1925).

DARWIN C., *Origin of Species.* London: John Murray (1st edn) (1859).

DARWIN C., *Origin of Species.* London: John Murray (4th edn) (1866).

DARWIN C., *The Descent of Man.* London: John Murray (1871).

DAY M.H., LEAKEY R.E.F., WALKER A.C. and WOOD B.A., *New hominids from East Rudolf, Kenya I.* « Am. J. Phys. Anthrop. », *42* (3), 461-476 (1975).

DAY M.H., LEAKEY R.E.F., WALKER A.C. and WOOD B.A., *New hominids from East Turkana, Kenya.* « Am. J. Phys. Anthrop. », *45*, 369-436 (1976).

DINGWALL W.O., *Reconstruction of the Parker/Gibson "model" for the evolution of intelligence.* « The Behavioral and Brain Sciences », 2, 383-384 (1979).

DOBZHANSKY T., *The Biology of Ultimate Concern.* New York: New American Library (1967).

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

DUBOIS E., *Sur le rapport du poids de l'encéphale avec la grandeur du corps chez les mammifères.* « Bull. Soc. d'Anthrop. de Paris », *8*, 337-376 (1897).

DUBRUL E.L., *Evolution of the Speech Apparatus.* Springfield: Thomas (1958).

DUBRUL E.L., *Development of the hominid oral apparatus.* In: « Morphology of the Maxillo-Mandibular Apparatus ». (ed. G.H. Schumacher) Leipzig: VEB Georg Thieme, 40-47 (1972).

DUBRUL E.L., *Origin and evolution of the oral apparatus.* « Frontier of Oral Physiology », *1*, 1-30 (1974).

ELDREDGE N. and GOULD S.J., *Punctuated equilibria: an alternative to phyletic gradualism.* In: « Models in Paleobiology ». (ed. T.J.M. Schopf), pp. 82-115. San Francisco: Freeman, Cooper (1972).

ELDREDGE N. and GOULD S.J., *Evolutionary models and biostratigraphic strategies.* In: « Concepts and Methods of Biostratigraphy ». (eds. E.G. Kauffman and J. Hazel), pp. 24-40. Stroudsburg, Pa.: Dowdan, Hutchinson and Ross (1977).

EWING J.F., *Ksar 'Akil.* « Antiquity », *21*, 186-196 (1947).

EWING J.F., *The treasures of Ksar 'Akil.* « Thought » (Fordham University), *24*, 255-288 (1949).

EWING J.F., *Current Roman Catholic thought on evolution.* In: « Evolution after Darwin ». pp. 19-28. Chicago: Chicago University Press.

FALK D., *Hominid brain evolution: the approach from paleoneurology.* « Yearbook of Physical Anthropology », *23*, 93-107 (1980a).

FALK D., *A reanalysis of the South African australopithecine natural endocasts.* « Am. J. Phys. Anthrop. », *53*, 525-539 (1980b).

FOUTS R.S., *Capacities for language in great apes.* In: « Socioecology and Psychology of Primates ». (ed. R.H. Tuttle), pp. 371-390. The Hague and Paris: Mouton (1975).

FURNESS W., *Observations on the mentality of chimpanzees and orangutans.* « Proceedings of the American Philosophical Society », *45*, 281-290 (1916).

GARDNER R.A. and GARDNER B.T., *Teaching sign language to a chimpanzee.* « Science », *165*, 664-672 (1969).

GESCHWIND N., *Disconnexion syndromes in animals and man.* Part I. « Brain », *88*, 237-294 (1965).

GOULD S.J., *Our greatest evolutionary step.* « Nat. Hist. », *88*, 40-44 (1979a).

GOULD S.J., *Panselectionist pitfalls in Parker and Gibson's model for the evolution of intelligence.* « The Behavioral and Brain Sciences », 2, 385-386 (1979b).

GOULD S.J. and ELDREDGE N., *Punctuated equilibria: the tempo and mode of evolution reconsidered.* « Paleobiology », *3*, 115-151 (1977).

HAYES K. and HAYES C., *The intellectual development of a home-raised chimpanzee.* « Proceedings of the American Philosophical Society », *95*, 105-109 (1951).

HAYES K. and HAYES C., *Imitation in a home-raised chimpanzee.* « Journal of Comparative and Physiological Psychology », *45*, 450-459 (1952).

HENRY J.L. and CLARKSON E.N.K., *Enrollment and coadaptions in some species of the Ordovician Trilobite genus,* Placoparia. « Fossils and Strata », *4*, 87-95 (1975).

HOLLOWAY R.L., *New australopithecine endocast, SK 1585, from Swartkrans, South Africa.* « Am. J. Phys. Anthrop. », *37*, 173-186 (1972).

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

HOLLOWAY R.L., *The endocast of the Omo L338y-6 juvenile hominid: gracile or robust Australopithecus?* « Am. J. Phys. Anthrop. », *54*, 109-118 (1981a).

HOLLOWAY R.L., *Revisiting the South African Taung australopithecine endocast: the position of the lunate sulcus as determined by the stereoplotting technique.* « Am. J. Phys. Anthrop. », *56*, 43-58 (1981b).

HOWELL F.C., *Hominidae.* In: « Evolution of African Mammals », (eds. V.J. Maglio and H.B.S. Cooke), pp. 154-248. Cambridge, Massachusetts: Harvard University Press. (1978).

HUXLEY Sir A.F., *Address of the President Sir Andrew Huxley at the Anniversary Meeting of the Royal Society,* London, 30 November 1981. « Proc. R. Soc. Lond. », A *379*, v-xx (1982).

HUXLEY J.S., *The three types of evolutionary process.* « Nature », *180*, 454-455 (1957).

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

ISAAC G.Ll., *The archaeological evidence for the activities of early African hominids.* In: « Early African Hominids ». (ed. C.J. Jolly), London: Duckworth (1978).

JOHANSON D.C., COPPENS Y. and TAIEB M., *Pliocene hominid remains from Hadar, Central Afar, Ethiopia.* In: « Les Plus Anciens Hominidés » (eds. P.V. Tobias and Y. Coppens), pp. 120-137. Colloque 6, 9e Congrès International des Sciences Préhistoriques et Protohistoriques, Nice, Septembre 1976 (1976).

JOHANSON D.C. and TAIEB M., *Plio-Pleistocene hominid discoveries in Hadar, Ethiopia.* « Nature », *260*, 293-297 (1976).

JOHANSON D.C. and WHITE T.D., *A systematic assessment of early African hominids.* « Science », *203*, 321-330 (1979).

JOHANSON D.C., WHITE T.D. and COPPENS Y., *A new species of the genus* Australopithecus (*Primates: Hominidae*) *from the Pliocene of eastern Africa.* « Kirtlandia », *28*, 1-14 (1978).

KEITH A., *New Discoveries Relating to the Antiquity of Man.* London: Williams and Norgate, pp. 1-512 (1931).

KELLOG D.E. and HAYS J.D., *Microevolutionary patterns in Late Cenozoic Radiolaria.* « Paleobiology », *1*, 150-160 (1975).

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

KNOTT J.F., *On the cerebral sinuses and their variations.* « J. Anat. and Physiol. », *16*, 27 (1882).

LEAKEY L.S.B., TOBIAS P.V., NAPIER J.R., *A new species of the genus* Homo *from the Olduvai Gorge.* « Nature », *202*, 7-9 (1964).

LEAKEY M.D., *Olduvai Gorge, Volume 3: Excavations in beds I and II 1960-1963.* London: Cambridge University Press, 1-300 (1971).

LEAKEY M.G. and BEHRENSMEYER A.K., *The hominid catologue.* In: « Koobi Fora Research Project » Vol. 1. (eds. M.G. Leakey and R.E.F. Leakey), pp, 86-182. Oxford: Clarendon Press (1978).

LEAKEY R.E.F. and WALKER A.C., Australopithecus, Homo erectus, *and the single species hypothesis.* « Nature », *261*, 572-574 (1976).

LIEBERMAN P., *On the evolution of language: a unified view.* In: « Primate Functional Morphology and Evolution ». (ed. R.H. Tuttle), pp. 501-540, The Hague/Paris: Mouton (1975).

MANN A.E., *The Paleodemography of* Australopithecus. PhD thesis, University of California, Berkeley (1968).

MANN A.E., *Some paleodemographic aspects of the South African australopithecines.* « Univ. Pennsylvania Publ. Anthrop. », *1*, 1-171 (1975).

MATHER K., *The genetical structure of populations.* « Symp. Soc. exp. Biol. », *7*, 66-95 (1953).

MATIEGKA H., *Über das Hirngewicht, die Schädelkapazität und die Kopfform, sowie deren Beziehungen zur psychischen Tätigkeit des Menschen.* « Sber. K. Böhm. ges. Wiss. », *20*, 1-75 (1902).

MONTAGU A., *The Human Revolution.* New York: Bantam Books (1965).

NEGUS Sir V.E., *The Biology of Respiration.* Edinburgh and London: E. and S. Livingstone (1965).

PAKKENBERG H. and VOIGT J., *Brain weight of the Danes.* « Acta anat. », *56*(4), 297-307 (1964).

PARKER S.T. and GIBSON K.R., *A developmental model for the evolution of language and intelligence in early hominids.* « The Behavioral and Brain Sciences », *2*, 367-381 (1979).

PEARL R., *Biometrical studies in man. I. Variation and correlation in brain weight.* « Biometrika », *4*, 13-104 (1905).

PETRIKOVA E., *Confluens sinuum, jeho utváření a variabilita.* « Acta. Univ. Carol. Medica », *7*, 619 (1963).

PILBEAM D., *The earliest hominids.* New York, Toronto, London: Bantam Books (1968).

PILBEAM D. and GOULD S.J., *Size and scaling in human evolution.* « Science », *186*, 892-901 (1974).

PREMACK A.J. and PREMACK D., *Teaching language to an ape.* « Scientific American », *227*, 92-99 (1972).

PREMACK D., *Language in chimpanzee?* « Science », *172*, 808-822 (1971).

RAK Y. and HOWELL F.C., *Cranium of a juvenile* Australopithecus boisei *from the lower Omo basin, Ethiopia.* « Am. J. Phys. Anthrop. », *48*, 345-366 (1978).

RENSCH B., *Evolution above the Species Level.* London: Methuen (1959).

REYMENT R.A., *Analysis of a generic level transition in Cretaceous ammonites.* « Evolution », *28*, 665-676 (1975).

SCHEPERS G.W.H., *The endocranial casts of the South African ape-men.* Part II of « The South African Fossil Ape-men, the Australopithecinae ». « Transv. Mus. Mem. », *2*, 167-272 (1946).

SCHMALHAUSEN I.I., *Factors of Evolution, the Theory of Stabilizing Selection* (Trans. I. Dordiek, ed. Th. Dobzhansky). Philadelphia: Blakiston (1949).

SCHREIDER E., *Brain weight correlations calculated from original results of Paul Broca.* « Am. J. Phys. Anthrop. », *25*(2), 153-158 (1966).

SCHWALBE G., *Ueber das Gehirnrelief der Schlaefengegend des menschlichen Schaedels.* « Z. Morph. Anthrop. », *10*, 1-93 (1907).

SIMPSON G.G., *Tempo and Mode in Evolution.* New York: Columbia University Press (1944).

SIMPSON G.G., *The Major Features of Evolution.* New York: Columbia University Press Press (1953).

SMITH G.E., *A new topographical survey of the human cerebral cortex, being an account of the anatomically distinct cortical areas and their relationship to the cerebral sulci.* « J. Anat. », *41*, 237-254 (1907).

SNELL O., *Die Abhängigkeit des Hirngewichtes von dem Körpergewicht und den geistigen Fähigkeiten.* « Arch. Psychiat. Nervenkr. », *23*, 436-446 (1891).

SNOWDON C.T. and FRENCH J.A., *Ontogeny does not always recapitulate phylogeny.* « The Behavioral and Brain Sciences », 2, 397-398 (1979).

SPANN M.W. and DUSTMANN H.O., *Das menschliche Hirngewicht und Seine Abhängigkeit von Lebensalter, Körperlänge, Todesursache und Beruf.* « Dt. Z. ges. gericht. Med. », *56*, 299-317 (1965).

THENIUS E., *Stammesgeschichte der Säugetiere (einschliesslich der Hominiden).* « Handbuch der Zoologie », Band 8: « Mammalia », Teil 2: « Lieferung », *47*, 1-368. Berlin: W. de Gruyter (1969).

TOBIAS P.V., Olduvai Gorge, Vol. 2: *The Cranium and Maxillary Dentition of* Australopithecus (Zinjanthropus) boisei. Cambridge: University Press, 1-264 (1967).

TOBIAS P.V., *The age of death among the australopithecines.* « The Anthropologist », Special Volume, pp. 23-28. (Univ. of Delhi, India) (1968a).

TOBIAS P.V., *The pattern of venous sinus grooves in the robust australopithecines and other fossil and modern hominoids.* « Anthropologie und Humangenetik » (K. Saller Festschrift), pp. 1-10. Stuttgart: Gustav Fischer Verlag (1968b).

TOBIAS P.V., *Brain-size, grey matter and race - fact or fiction?* « Am. J. Phys. Anthrop. », *32*(1), 3-26 (1970).

TOBIAS P.V., *The Brain in Hominid Evolution.* New York/London: Columbia Univ. Press, i-xv and 1-170 (1971a).

TOBIAS P.V., *The distribution of cranial capacity values among living hominoids.* « Proc. III Internat. Congr. Primat., Zurich 1970 », Vol. I, pp. 18-35 (1971b).

TOBIAS P.V., *Homo erectus.* In: « Encyclopaedia Britannica » (15th edn), Vol. 8, 1030-1036 (1974a).

TOBIAS P.V., *Aspects of pathology and death among early hominids.* « The Leech », *44*(3): 119-124 (1974b).

TOBIAS P.V., *Brain evolution in the Hominoidea.* In: « Primate Functional Morphology and Evolution ». (ed. R.H. Tuttle), 353-392. The Hague: Mouton Publishers (1975a).

TOBIAS P.V., *Long or short hominid phylogenies? Paleontological and molecular evidences.* Chapter 6 in: « The Rôle of Natural Selection in Human Evolution ». (ed. F. Salzano), 89-118. Amsterdam/Oxford: North-Holland Publishing Co., 1-439 (1975b).

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

TOBIAS P.V., *L'évolution du cerveau humain.* « La Recherche », *11*(109), 282-292 (1980).

TOBIAS P.V., *The emergence of man in Africa and beyond.* « Phil. Trans. R. Soc. », *292*, 43-66 (1981).

TOBIAS P.V., *The evolution of the human brain, intellect and spirit.* 1st Andrew Abbie Memorial Lecture, Adelaide: University Press (1982a).

TOBIAS P.V., *Olduvai Gorge,* Vol. 4: *Homo habilis.* Cambridge: University Press, pending (1982b).

VOLLERT C., *Evolution and the Bible.* In: « Symposium on Evolution », 81-119, Pittsburgh: Duquesne Univ.

WEIDENREICH F., *Observations on the form and proportions of the endocranial casts of* Sinanthropus pekinensis, *other hominids and the great apes: a comparative study of the brain size.* « Palaeont. sin. D. », 7, 1-50 (1936).

WEIDENREICH F., *The skull of* Sinanthropus pekinensis. « Palaeont. sin. », *127*, 1-486 (1943).

WHITE T.D., JOHANSON D.C. and KIMBEL W.H., Australopithecus africanus: *its phyletic position reconsidered.* « S. Afr. J. Sci. », *77*, 445-470 (1981).

WOODHALL B., *Variations of the cranial venous sinuses in the region of the torcular Herophili.* « Archiv. Surg. », *33*, 297 (1936).

WOODHALL B., *Anatomy of the cranial blood sinuses with particular reference to the lateral.* « Laryngoscope », *49*, 966 (1939).

WOOD JONES F., *The nature of the soft palate.* « J. Anat. », *74*, 147-170 (1940).

WYNN T., *The intelligence of Oldowan hominids.* « Journal of Human Evolution », *10*, 529-541 (1981).

MOLECULAR BIOLOGY AND THE STUDY OF PRIMATE EVOLUTION

RUSSELL F. DOOLITTLE
Department of Chemistry University of California, San Diego
La Jolla, California, U.S.A.

Abstract

During the past 30 years vast amounts of molecular biological data have been accumulated that deal with evolution. The overwhelming majority of these data have been supportive of previous efforts hased on traditional approaches to the problems of phylogenetic relationships. In a few instances there have been disagreements, primarily quantitative, between classical views and the conclusions drawn by molecular biologists. As a case in point, the divergence time for lines leading to chimpanzees and gorillas, on the one hand, and humans, on the other, was thought to be 15-30 million years ago. In the 1960's immunochemical data led biochemists to suggest that common ancestry must have existed much more recently than that. Indeed, much of the subsequently obtained amino acid sequence data seems consistent with a divergence time of 5-10 million years ago, if not less. Tools are now at hand whereby all these disputes ought to be resolved, providing a systematic application of appropriate techniques to a well chosen set of extant specimens can be achieved. In particular, the cloning and sequencing of the primate pseudogene termed "pseudogene alpha-1" from the five genera of non-human hominoids and a representative specimen of old world monkey ought to provide sufficient data to resolve the issue.

Introduction

Scarcely thirty years have passed since the discovery that DNA is the genetic material of virtually all living organisms. In that brief interval massive amounts of molecular data have been accumulated that in one way or other can be brought to bear on the study of evolution. In particular, amino acid sequence data and then, more recently, DNA sequences, have lent themselves to the reconstruction of phylogenetic relationships. The advantage of these data over traditional characterization involving morphology, physiology, embryology, etc., is that they are digital reflections of the mutational events themselves; they are the quanta of biology. As such, more than in any other application of numerical taxonomy, they can be used with great objectivity in establishing relationships. Such sequence data also fit well with the use of computers. Phylogenetic trees and networks can be constructed with no preconceived bias on the part of the investigator as to the nature of the relationship.

Most of the sequence data collected so far have been consistent with the phylogenies that were assiduously constructed by generations of biologists using paleontological and morphologic data, as well as observations from a host of other disciplines. For the most part, the disagreements have been trivial compared with the agreements and substantiation. But even minor disagreements seem to take on an exaggerated importance when it comes to the evolution of man, and the molecular biological data established in the area of primate phylogeny have been the subject of intense scrutiny and debate.

Briefly put, the classical view of hominoid evolution has been that man diverged from his closest extant kin, chimpanzees and gorillas, 15-30 million years ago. The molecular data, as first realized from quantitative immunological measurements, suggest a much more recent divergence, 5-10 million years ago or, perhaps, even less. In this article I will review briefly the basis of the dispute and its current status, and then suggest a set of molecular biological measurements that ought to be able to resolve the issue with finality.

Man-Ape Divergence Times: A Dispute

It was Goodman (1961; 1963) who first recognized that immunological measurements were at odds with the classical picture of how closely man was related to chimpanzees and gorillas. His carefully collected data placed man squarely in a grouping with those creatures, and, more to the point, they suggested that either molecular evolution had slowed down among these hominoids or that they had diverged more recently than was thought. He felt that the former was more likely, and suggested that some kind of isoimmunization phenomenon was occurring as a result of the hemochordial circulation that exists in placental mammals.

The cudgel was quickly picked up by Sarich and Wilson (1966; 1967), who felt it much more likely that the fossil record, scant as it was for higher primates, was in error, and that man was indeed much more recently diverged from the apes than had been thought. This view was not well received by paleontologists (Leakey, 1970). A number of suggestions were made in an effort to resolve the discrepancy, including the possibility that the apparent slowdown in the change of proteins in higher primates was the result of longer generation times (Laird *et al.*, 1969); the matter was not easily resolved (Sarich and Wilson, 1973; Doolittle, 1979).

Although the original data provoking the dispute were immunological, the subsequent accumulation of amino acid sequence data has been consistently of the same ilk. Either the divergence times have been misjudged by paleontologists, or the molecular clock has slowed down in higher primates. In the following paragraphs I am going to examine amino acid and DNA sequence data only, to the exclusion of immunological ond other molecular approaches, such as DNA hybridization. I will attempt to show why these data haven't yet settled the matter, but at the same time propose a strategy that may yet answer the question unequivocally.

Amino Acid Sequence Studies on Primate Proteins

More than a hundred different human proteins have had their amino acid sequences determined during the past 25 years (Dayhoff, 1978; Doolittle, 1981). The number of sequences determined for non-human primates is considerably smaller, of course, although in the cases of a few proteins, a variety of primates has been studied. I have in mind especially the various globin chains, fibrinopeptides, alpha crystallins and carbonic anhydrases. To the best of my knowledge, in only the case of myoglobin and the fibrinopeptides have representatives of all major primate families been studied. In these two cases the data are fairly consistent, the number of amino acid replacements observed along various branches being very similar in both proteins (Fig. 1). Even when taken together, however, the numbers of amino acid interchanges are too small to make a significant judgment about the precise branching times of the higher primates. Barely a half dozen differences exist among the great apes in the cases of these two proteins.

The two proteins exemplify a feature of amino acid sequence data that is important for phylogenetic studies; namely, the more dispensable a structure, the more rapidly it can change (Doolittle, 1979). Thus, although the fibrinopeptides are composed of only one fourth the residues

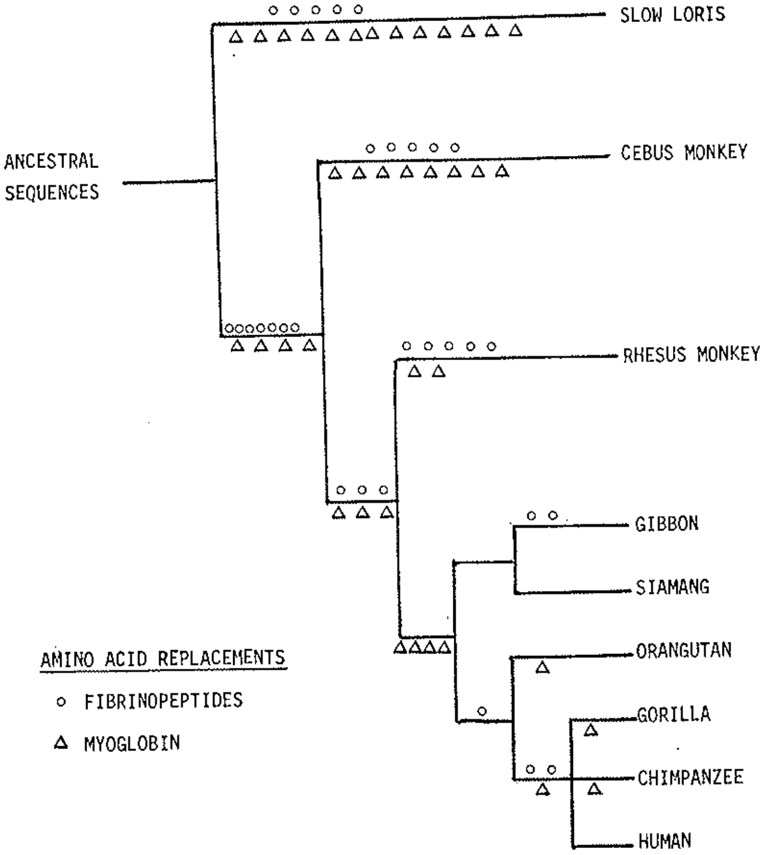


FIG. 1. Amino acid replacements in two different proteins occurring along lineages leading to some primates. The myoglobin data are from Dene *et al.* (1980) and the fibrinopeptide data from Wooding and Doolittle (1972).

of myoglobin, the number of observed changes is about the same. Another way of putting it is that fibrinopeptides change about four times more rapidly than myoglobins. What we see, however, is that even this free-wheeling protein is inadequate for providing a molecular basis for setting divergence times among higher primates. What is needed is something that changes even faster, and for that we are forced to turn to DNA sequences.

A Suggested Strategy

The primate genome consists of approximately 100 million nucleotide pairs. If the entire base sequence were known for each of the extant hominoids, it is likely that, at the very least, an unequivocal branching order could be constructed for the higher primates. Moreover, with such a preponderance of data it would seem reasonable that the branch lengths could be quantitatively evaluated and the chronological dispute resolved. Given the impracticality of determining every possible sequence, let us consider which sequences would be most useful from the point of view of systematics. In the case of protein sequences, it has been useful to choose proteins according to how rapidly they change in accordance with how distantly related are the creatures being compared. If the comparison is between very distantly related organisms, then a persistently slow changing protein is desirable. For example, cytochrome sequences can be used to construct phylogenetic trees extending across the animal and plant kingdoms, and microbes also. On the other hand, the more closely related the organisms involved, the more desirable it is to have a fast-changing molecule so that statistically significant numbers of changes are observed. Thus, the rapidly changing fibrinopeptides have been useful in relating mammals at the order level. But at the level of genus, even these fast changers are often inadequate to the task.

Our strategy has two aspects that must be considered. First, what molecules or gene segments should we examine, and, then, what organisms should we study? Let us take up the second aspect first.

Choice of Primates for Study

Molecular biologists have not been as systematic as they might during the initial assault on the problem of various primate relationships. Thus, although a reasonable number of primate proteins has been sequenced, the attack has been scattered. For example, among the old world monkeys the choice of specimen has been virtually random. There are 16 genera of these monkeys, and if general agreement on a single choice could be made, the data obtained would be more meaningful. At this point there are more sequences available from the rhesus monkey than for any of the others, and for that reason I suggest that further sequence studies focus on that creature when old world monkey data are needed.

Sequence studies on new world monkey proteins have also been sparse and inconsistent with regard to what specimens were studied. Of the 12 existing genera, three different studies have managed to select three different ones. In defense of these previous investigations, let me emphasize how difficult it is for biochemists to obtain non-human primate material. This is especially true if the protein to be studied needs substantial amounts of blood or tissue. Recombinant DNA techniques can be accomplished starting with relatively small amounts of liver or white blood cells, however, and once the material is cloned, it can serve as a perpetual source.

Choice of Molecule for Sequencing

As noted above, the more relaxed the restrictions are on a portion of a genome, the faster it will change and the more useful it will be for close relationships. At the DNA level the choices we have are threefold. First, we could examine the "third base" changes in the gene for any chosen protein, since many of these are "silent" mutations, which is to say, nucleotide substitution does not change the corresponding amino acid in the gene product. There are many data in the literature that testify to the fact that these nucleotide positions change at a rate significantly faster than those at codon positions 1 and 2, no matter what the gene (Kimura, 1981). Or we could choose to look at specified introns, those intervening sequences in genes that are not ordinarily expressed. These nucleotide strings also change at a rate that is apparently close to full throttle, i.e., selection or rejection play a negligible role in their survival. (Occasional substitutions might be rejected, either because splicing junctions are impaired or new ones invented, for example, or for other reasons of expression control).

The sequences that are the best for study, however, are those of so-called pseudogenes. Pseudogenes are segments of DNA that resemble genes for known polypeptide chains but which, because of critical nucleotide replacements leading to errors in stopping or starting polypeptide synthesis, or frameshift errors, cannot be expressed. They usually lie close to the normal genes from which they have sprung by gene duplication. Recent studies (Li *et al.*, 1981; Miyata and Hayashida, 1981) have revealed that pseudogenes evolve at a very rapid rate compared with their expressed counterparts. Moreover, all three nucleotide positions in the codons change at the same rate, suggesting an entirely relaxed situation with regard to selection/rejection. Indeed, the rate of change ought to be the same for *all* pseudogenes. As such, pseudogenes are ideal for studying closely related organisms.

It is known that humans have a pseudogene for the alpha chain of hemoglobin. This segment can be easily identified, since the globin chains have been extensively characterized by recombinant DNA methods, and the surrounding genomic terrain is well explored. Thus, the globin alpha chain gene region of the human genome contains five alpha chain-like sectors (Lauer *et al.*, 1980). Two of these correspond to apparently identical copies of the genes for adult hemoglobin alpha chains. Two others are genes for embryonic alpha chains, and the fifth to a non-expressed alpha chain *pseudogene*. A similar situation exists for a cluster of human globin beta chain genes, although in this case there is only a single active gene for the adult chain (Efstratiadis *et al.*, 1980).

It is estimated that the human alpha-1 pseudogene is the result of a gene duplication that occurred about 50 million years ago, the change that rendered it non-expressible occurring shortly thereafter (Li *et al.*, 1981. This estimate is based on presently accepted divergence times for mice and humans and considerations of the observed rates of change for ordinary globin alpha chain genes. If the estimates are accurate, all old world monkeys and apes ought to carry the DNA segment. What I would propose then, is that the globin alpha-1 pseudogene be cloned and sequenced from the other hominoids and from the rhesus monkey. The number of observed changes ougbt to be large enough to allow an unequivocal computer-generated phylogeny to be established. Moreover, if the rate of change is as constant as alleged, then the absolute divergence times can be calculated with reasonable precision.

I have made some predictions as to the numbers of nucleotide replacements that would be expected (Table I). These estimates were made by using the pseudogene nucleotide replacement rate calculated by Li *et al.* (1981), and by assuming divergence times for the higher primates judged to be reasonable by this working group (see, e.g., Pilbeam, 1982, and

Greenfield, 1982). In any event, the new data themselves ought to provide a most reliable nucleotide replacement rate and self-setting clock, if the divergence time for *any* pair can be agreed upon. At the same time the data should reveal any grossly anomalous divergence times.

Experimental Priorities

Although the technology for isolating the globin alpha chain gene cluster is straightforward now that the human genes have been cloned, this is not to say that the work itself is trivial. Accordingly, there are desirable orders of priority for undertaking the experiments. For example, a very high priority would be the isolation of the alpha-1 pseudogene from old world monkeys, if only to establish that the pseudogene exists in these animals. It would also be reassuring to see that the number of nucleotide

TABLE I - *Nucleotide differences among the alpha globin genes of higher primates.*

OBSERVED CHANGES IN ALPHA CHAINS

	Rhesus Monkey	*Gibbon/ Siamang*	*Orangutan*	*Gorilla*	*Chimpanzee*	*Man*
Rhesus Monkey		—	8	5	5	5
Gibbon/Siamang	100 ± 5		—	—	—	—
Orangutan	100 ± 5	64 ± 5		3	3	3
Gorilla	100 ± 5	64 ± 5	48 ± 5		0	0
Chimpanzee	100 ± 5	64 ± 5	48 ± 5	30 ± 4		0
Man	100 ± 5	64 ± 5	48 ± 5	30 ± 4	20 ± 4	

PREDICTED NUCLEOTIDE DIFFERENCES AMONG PSEUDO-ALPHA-1 GENES *

* The predictions are based on divergence times of 28, 17, 13, 8 and 5 million years ago, respectively, and a pseudogene replacement rate of 5×10^{-9} per nucleotide per year for 400 nucleotide comparisons. The product of the divergence time and overall ($n=400$) replacement has been multiplied by 2 to take account of both lineages in each comparison. Estimates have been corrected for multiple-hits and back-mutations, but no consideration has been given to differences in rate for transitions as opposed to transversions.

replacements, when compared with the human sequence, was not too far from the predictions in Table I.

If the rhesus monkey study gives the expected results, then the next step ought to be isolation of the pseudogene from chimpanzee. Indeed, the human-chimpanzee relationship could be immediately gauged in terms of the monkey-human results. The addition of data from gorilla would then be of great interest, the divergence order in this case being of as much interest as the divergence times.

Of lesser priority, but of great importance, nonetheless, would be the obtaining of the sequences from the orangutan and gibbon or siamang alpha-1 pseudogenes. Apart from giving information about when these lineages diverged, the data would allow for a greater degree of confidence in all the previous comparisons, since computer-generated phylogenetic trees would now reveal whether or not the rates of change had been genuinely constant along all lineages.

Finally, a new world monkey alpha chain gene cluster could be examined. If present estimates about when the alpha-1 pseudogene appeared are correct, and if paleontologists have accurately judged when new world monkeys diverged from the lines leading to higher primates, then these creatures should not have this particular pseudogene. If they should have it (or possibly its expressible antecedent), another valuable checkpoint would be available for setting the clock.

In conclusion, it is altogether possible that these experiments could settle the debate as to when the lineage leading to man branched off from those leading to existing apes. At the same time it would establish an independently derived phylogeny for all the higher primates. In the end, of course, we would expect the paleontological and the molecular biological results to be in complete harmony.

REFERENCES

Dayhoff M. O., *Atlas of Protein Sequence and Structure*. National Biomedical Research Foundation, Washington, D.C., Vol. 5 and Supp. 1-3 (1978).

Dene H., Sazy J. and Romero-Herrera A. E., « Biochim. Biophys. Acta », *625*, 133-145 (1980).

Doolittle R. F., in *The Proteins* (H. Neurath and R. L. Hill, eds.) Academic Press, New York, 2nd edition, Vol. 4, pp. 1-118 (1979).

Doolittle R. F., « Science », *214*, 149-159 (1981).

Doolittle R. F., Wooding G. L., Lin Y. and Riley M., « J. Mol. Evol. », *1*, 74-83 (1971).

Efstratiadis A., Posakony J. W., Maniatis T., Lawn R. M., O'Connell C., Spritz R. A., De Riel J. K., Forget B. G., Weissman S. M., Slightom J. L., Biechl A. E., Smithies O., Baralle F. E. and Shoulders C. C., « Cell. », *21*, 653-668 (1980).

Goodman M., « Human Biol. », *33*, 131-162 (1961).

Goodman M., « Human Biol. », *35*, 377-406 (1963).

Greenfield L., Chapter in this volume (1982).

Kimura M., « Proc. Natl. Acad. Sci., U.S.A. », *78*, 5773-5777 (1981).

Laird C. D., McConaughy B. L. and McCarthy B. J., « Nature (Lond.) », *224*, 149-154 (1969).

Lauer J., Shen C.-K. J. and Maniatis T., « Cell », *21*, 119-130 (1980).

Leakey L. S. B., « Proc. Natl. Acad. Sci., U.S.A. », *67*, 746-748 (1970).

Li W.-H., Gojobori T. and Masatoshi N., « Nature (Lond.) », *292*, 237-239 (1981).

Miyata T. and Hayashida H., « Proc. Natl. Acad. Sci., U.S.A. », *78*, 5739-5743 (1981).

Pilbeam D., Chapter in this volume (1982).

Sarich V. M. and Wilson A. C., « Science », *154*, 1563-1566 (1966).

Sarich V. M. and Wilson A. C., « Science », *158*, 1200-1203 (1967).

Sarich V. M. and Wilson A. C., « Science », *179*, 1144-1147 (1973).

Wooding G. L. and Doolittle R. F., « J. Hum. Evol. », *1*, 553-563 (1972).

FOSSIL PROTEINS AND EVOLUTIONARY TIME

JEROLD M. LOWENSTEIN
University of California
San Francisco

ABSTRACT

Discoveries in molecular biology during the past decade have provided powerful new ways of estimating the genetic relations and evolutionary divergence times of living species. A radioimmunoassay technique has been devised for obtaining comparable information on extinct species, from the residual proteins in their fossils. This technique has been applied to elephant, marsupial, human and hominoid fossils. Data obtained in this way provides evidence independent of tooth and bone morphology for the affinities of extinct and living groups.

We are in the midst of three scientific revolutions affecting our ever-changing image of man's place in nature. The first is the cosmological revolution, triggered by recent discovery of the cosmic background radiation. This cosmic background was presumably generated by the Big Bang with which our universe began some twenty billion years ago — and so, in tune with this presentation, we may consider the background radiation as consisting of fossil photons twenty billion years old [39]. The second revolution is plate tectonics, better known as continental drift. As ridiculous as it seemed when first proposed more than half a century ago, there is now overwhelming evidence that the continents have moved quite far from their initial position when the earth was formed about four and a half billion years ago, and they are still moving [6, 44]. By radiometric dating methods [19], we can identify those geologic formations which are oldest, and in them evidence of life that existed three and a half billion years ago has been discovered. Continental drift helps to explain the present global distribution of living forms as well as fossil groups. The third revolution, and the one I will be mainly concerned with here, is the explosion of knowledge in molecular biology that started with Watson and Crick's discovery of the double helical structure of the genetic material which determines what forms life on earth shall take [42].

These three revolutions have in common the discovery that some familiar, taken-for-granted feature of the world, that seemed stable and dependable, is in fact changing irreversibly. The stars and galaxies which appear so steady in the night sky are hurtling apart. The solid land on which we walk is drifting like chunks of eggshell on a viscous spheroid. All of earth's living creatures, from bacteria to leviathans, are evolving and changing from generation to generation. The new discovery is that the molecules of which each organism is made are changing much more rapidly than we had previously believed. For decades it has been thought that *any* molecular change in the genetic material would result in detectable change in the organism — that the overwhelming number of such changes would be deleterious to survival and would not persist, but that the occasional mutation would enhance survival, be favored by natural selection, and become fixed in the gene pool.

During the past decade, evidence has been piling up that this view of how the genes work is wrong. The DNA of which genes are made determines the proteins of which organisms are made. Every three DNA bases (triplet) can determine one amino acid in the protein sequence. But because of the redundancy of the genetic code, there can be DNA base-pair mutations, especially in the third position of the triplet, which do not result in an amino acid change [4, 22, 23]. Even more recently, it has been learned that long stretches of eukaryotic DNA do not encode any proteins at all: these stretches have been called intervening sequences or "introns", in contrast with the expressive DNA or "exons". Because this DNA replicates itself but does not, as far as we know, contribute to shaping the organism, it has been termed "selfish" or "parasitic" DNA [15, 27, 32]. Like the "silent" codons of DNA which can change without changing amino acid sequences, "selfish" DNA can undergo mutations without any apparent effects on organismal biochemistry. Since these DNA mutations neither enhance nor diminish fitness, it might be expected that they would survive in living organisms more frequently than mutations which do result in biochemical alteration — and there is now a good deal of evidence that "silent" DNA is evolving at three or four times the rate of expressive DNA [22, 24, 27].

What is even more remarkable than "silent" DNA changes is the amount of expressive DNA change, resulting in different protein amino acid sequences, which apparently "makes no difference" to the organism. Every protein which has been studied — cytochrome c, collagen, hemoglobin, albumin, fibrinopeptides, to name only a few — has been found to undergo evolutionary changes in its amino acid sequences at a rather steady rate, over millions of years; yet there is no evidence that horse cytochrome works "better" or "worse" than that of blue-green algae or that human collagen is stronger or weaker than that of sponges.

These amazing and unexpected discoveries in molecular biology and in evolutionary biochemistry have given rise to two entirely new and related concepts: "neutral" mutation and the molecular clock. Kimura [23] advanced the neutral mutation theory to explain how it is that so much molecular evolution takes place without apparently affecting organismal fitness. He estimated that only about one out of twenty mutations affects fitness. Many workers in molecular evolution more or less independently deduced that changes in protein sequence or in DNA bases represent a kind of clock for timing evolutionary divergences [2, 9, 10, 11, 12, 15, 22, 23, 35, 38, 43]. If this be true, each living creature on earth has within its tissues a kind of molecular Rosetta Stone from which its evolutionary history can be read, once the code is broken.

Just as radiometric dating of archeological deposits has proved far more reliable than the guesses used previously, based on conjectural rates of sedimentation from lakes and rivers, for instance, and often wrong by orders of magnitude, so a molecular clock approach should be much more accurate than speculations about the time needed for evolving groups to achieve certain measurable morphological differences. It is well known that morphological evolution can occur relatively rapidly, as in the very diverse radiation of mammals during the past 70 million years, or very slowly, as with reptiles like the crocodiles and turtles, which have changed relatively little in a time span of two hundred million years [48]. Wilson has noted [43], "Species of frogs that are similar enough to be included within a single genus can differ as much at the sequence level as does a bat from a whale". The very frequent occurrence of convergent and parallel evolution can bring unrelated groups to resemble each other in one or more morphological characteristic, but there is no evidence that convergence occurs on the molecular level.

But the notion of "molecular clocks" has aroused great controversy and has been much disputed by paleontologists who do not like the times suggested by these clocks [2, 8, 18, 20, 37, 40, 47]. To some of these paleontologists, resemblances between the teeth of fossil groups removed millions of years in time from each other are more impressive evidence of genetic affinity than a mass of molecular data which suggests otherwise. As has so often been the case with evolutionary disputes, starting with Darwin, some of the most heated controversy about molecular clocks focuses on human origins.

In the 1960's it was widely (but not universally) believed among professional anthropologists that the human lineage had been separate from that of the apes for at least twenty million years and that the Miocene hominoid *Ramapithecus*, of Asian-European-African distribution, was on the direct line to modern humans [40]. Comparison of ape and human DNA and proteins, however, has shown that living humans are about 99% identical genetically to chimpanzees and gorillas; in molecular time, this is about five million years [9, 25, 35, 36]. If humans and African apes diverged only five million years ago, *Ramapithecus*, dated between eight and fourteen million years, could not be human.

About five years ago, when this debate was very intense, it occurred to me that one might be able to resolve the issue if one could test the resemblance of *Ramapithecus* proteins to those of living apes and humans. It had been reported that amino acids and insoluble proteins such as collagen sometimes survive in fossils millions of years old [45]. I developed a very sensitive radioimmunoassay for detecting fossil proteins and comparing them immunologically to those of their living relatives [28]. Next, I had to demonstrate that there are detectable proteins in fossils and that, despite thousands or millions of years of chemical breakdown and leaching, they retain enough of their original immunological character to provide usable genetic information.

A frozen Siberian mammoth provided the ideal test. We know that proteins are best preserved at low temperatures. The baby mammoth known as Dima was discovered near Magadan, USSR, in 1977 and refrigerated immediately, to prevent tissue deterioration. The radiocarbon date was 44,000 years. The evolutionary biochemistry group at Berkeley, with whom I collaborated, obtained a specimen of thigh muscle and extracted it with buffer solutions. Rabbits injected with this extract produced antisera which reacted with elephant albumin [34]. Radioimmunoassay demonstrated the presence of elephant-like albumin in the tissue extract, about one percent as much as one would obtain from fresh muscle [30]. It was even possible to show how closely related mammoth albumin is to the albumins of the living elephants: it is very similar to both, and about equally distant from them, suggesting a "molecular clock" divergence time of about three million years. These findings are generally consistent with paleontological opinion [7], though the divergence time is somewhat more recent than the usual estimation of about five million years.

No one has questioned that the woolly mammoth (*Mammuthus primigenius*) was an elephant. The fossil protein results confirmed that proteins as old as 44,000 years may preserve good species-specificity and may provide information about genetic closeness and divergence times. Next, the method was applied to resolving a true evolutionary dispute, in which different paleontologists strongly disagreed about the phylogenetic position of a recently extinct species.

The Tasmanian wolf (*Thylacinus cynocephalus*), a marsupial carnivore of Australia that was eradicated within recent memory by European settlers, has been considered by most systematists to be related to the dasyurids, the diverse group of Australian marsupi-carnivores that includes the native cat (*Dasyurus*), the kowari (*Dasyuroides*) and the Tasmanian devil. As its name implies, the Tasmanian wolf is very convergent morphologically with true wolves. But there is yet another convergent marsupial wolf, a South American fossil genus, *Borhyaena*, which bears strong dental and skeletal resemblances to *Thylacinus*. Based on forty-five dental and cranial measurements, Archer [1] concluded that *Thylacinus* is more closely related to *Borhyaena* than to any of the dasyurids. According to our present understanding of plate tectonics, Australia and South America separated about seventy million years ago, so that the *Thylacinus-Borhyaena* divergence must be assumed at least that old.

Skin and muscle specimens of Tasmanian wolf were obtained from Australian museums, the specimens were extracted with buffers, and the extracts were tested by radioimmunoassay, using antisera to numerous marsupial albumins. *Thylacinus* albumin proved to be quite similar to those of the dasyurids, *Dasyurus* and *Dasyuroides* — estimated divergence 6-10 million years. *Borhyaena* material was not available for comparison, but all the Australian species tested were much closer to each other than any was to the South American opossums, as would be expected from the geographical considerations of plate tectonics. The case of the Tasmanian wolf demonstrates forcefully that dental and skeletal resemblances are unlikely to provide reliable measures of evolutionary time, or even of evolutionary relationships.

Albumin is an excellent protein for studying immunological relations among living and recently extinct species [18, 36]. But albumin is highly soluble in water, and most fossils are exposed to water during some periods of time, so that fossils older than a few thousand years rarely have detectable albumin. For this reason, I have concentrated on finding collagen in the older fossils. Collagen, the main protein of skin, bone and other connective tissue, is a triple helix of about 3000 amino acids [3, 16], sufficiently resistant to water and other environmental agents that it can often be identified in fossils hundreds of thousands or millions of years old [45]. Because collagen is a conservative protein and all mammalian collagens are very similar, collagen injected into rabbits or other experimental animals does not evoke antisera of as high titer as more rapidly evolving proteins like albumin [17]. Nevertheless, I have been able to detect collagen in a number of human fossils (Fig. 1), including an Egyptian mummy, Cro-magnon, neanderthal, *Homo erectus*, and *Australopithecus* [28, 29, 31]. These fossil collagens react more strongly with antisera to human collagen than with antisera to other mammalian collagens such as bovine and rat collagen, which indicates that the fossil material has retained some of its species-specificity. A problem in working with primate, and particularly hominid, fossils, is that they are so rare and precious that only milligram quantities are available. This would be more than adequate for living or recently extinct tissue, but the amount of protein diminishes markedly with time. Many old fossils give such weak reactions that concentration techniques are necessary, and these are not possible with very small amounts of fossil material.

As I remarked earlier, it was the *Ramapithecus* controversy that first aroused my interest in studying fossil proteins, as a way of attempting to resolve the issue whether *Ramapithecus* was a hominid (in which case its proteins should be more like human than ape proteins) or whether it was an ape (in which case its proteins should be equally similar to those of humans and apes). From Professor David Pilbeam, I was able to obtain small fragments of two *Ramapithecus* and three *Sivapithecus* specimens. I dissolved these in an EDTA buffer and tested the extract with antisera to various primate albumins and collagens. No significant reactions were observed.

A second approach to fossil immunology, which worked initially with the mammoth extract, is to inject the fossil material into rabbits and hope

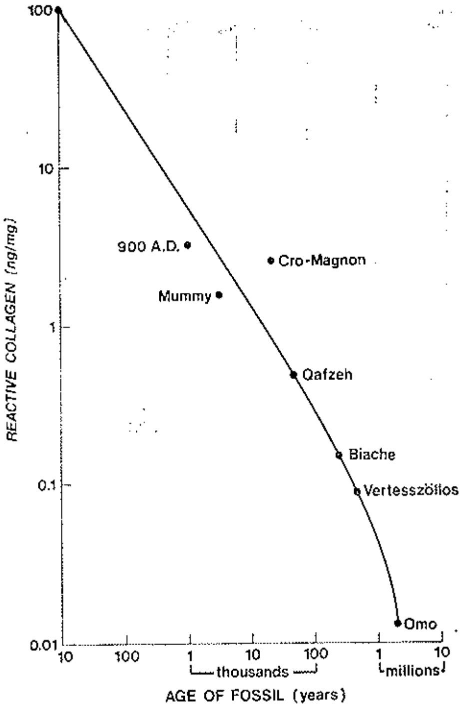


FIG. 1. Collagen in human fossil bones, detected by radioimmunoassay (ng collagen per mg bone). 900 A.D. (Hungarian burial); Mummy (Egyptian 800 B.C.); Cro-Magnon (Musée de l'Homme, Paris); Qafzeh (Neanderthal, Israel); Biache (*Homo erectus*, France); Verteszöllos *Homo erectus*, Hungary); Omo (*Australopithecus robustus*, Ethiopia).

that the rabbit will produce species-specific antibodies against the proteins of living species. Having failed to get direct reactions with the *Ramapithecus/Sivapithecus* material, I pooled the small amount that was left and injected it into a rabbit. The rabbit anti-fossil serum was then tested against the sera of various primate and nonprimate species (Fig. 2). These results were compared with reactions obtained from injecting into rabbits fossil material from a 3000 year old Egyptian mummy and 500,000 year old *Homo erectus* from Verteszöllos.

Antisera to mummy and *Homo erectus* reacted as expected: most strongly with human serum, somewhat less strongly with chimpanzee and gorilla serum, less still with sera of the Asian apes, the chimpanzee and gibbon, and only weakly with the sera of monkeys and other mammals.

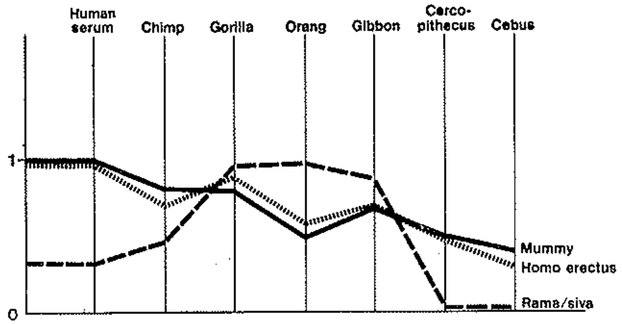
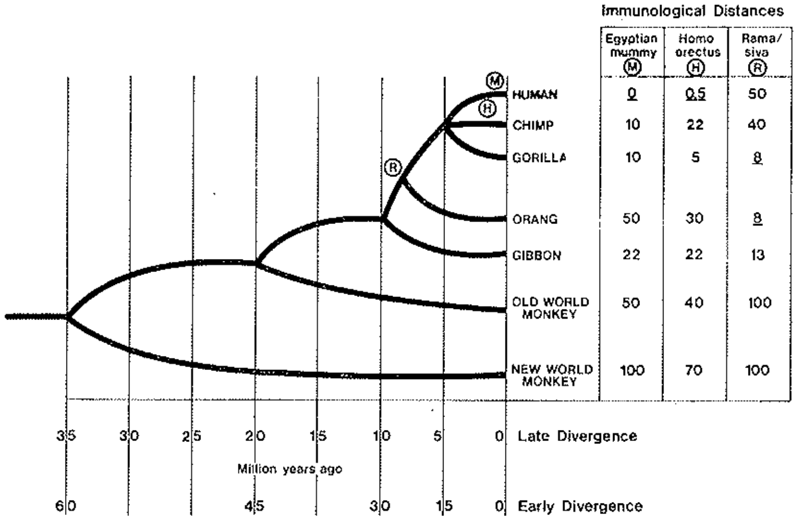


FIG. 2. Serum-specific reactions of antibodies made in rabbits to extracts of three different hominoid fossils: Egyptian mummy (800 B.C.), *Homo erectus* (Verteszöllos, 500,000 B.P.), a mixture of five fragments of *Ramapithecus* and *Sivapithecus* from the Siwalik, Pakistan. Antisera to mummy and *Homo erectus* react most strongly with human serum, as expected of human proteins. *Ramapithecus/Sivapithecus* antiserum gives a very different pattern of reactions, showing more affinity for Orang, Gorilla and Gibbon than for human and chimp sera.

Antisera to *Ramapithecus/Sivapithecus* gave a very different pattern of reactions, binding most strongly to orang, gibbon and gorilla sera, less strongly to chimpanzee and human sera, and only weakly with the sera of monkeys and other mammals.

From these results, one can conclude that *Ramapithecus/Sivapithecus* was hominoid, as closely related to the Asian as to the African apes, and definitely no closer to modern humans than to the chimpanzee. The strong reaction with gorilla serum seems to be a paradox, as gorilla, chimpanzee and human proteins generally react more like each other than like orang or gibbon proteins. I cannot explain these findings. Obviously much more work, on more fossils, is necessary. This single result is unsatisfactory for other reasons. The injected fossil material was contaminated with egg protein, which is used in the radioimmunoassay to block nonspecific reactions. I do not know how this may affect the pattern of reactions, though I cannot see how anti-egg protein would react more strongly with hominoid than with monkey or other sera. More likely, the egg protein acted as an adjuvant stimulating antibody formation against the small amount of fossil protein material present. Certainly it would be desirable to make antisera against individual *Ramapithecus* and *Sivapithecus* fossils rather than a mixture of specimens.

If one accepts these results as valid and looks for the best fit of the *Rama/Siva* reactions with the hominoid family tree constructed from



Immunological Distances

	Egyptian mummy Ⓜ	Homo erectus Ⓗ	Rama/siva Ⓡ
HUMAN	0	0.5	50
CHIMP	10	22	40
GORILLA	10	5	8
ORANG	50	30	8
GIBBON	22	22	13
OLD WORLD MONKEY	50	40	100
NEW WORLD MONKEY	100	70	100

FIG. 3. Best placement of the antisera in Fig. 2 on the molecular phylogeny of the hominoids. Mummy and *Homo erectus* clearly fall on the human lineage. *Ramapithecus/Sivapithecus* fits best at the divergence of orang and African apes. As these latter fossils are known to be about 8 million years old, their position tends to support a "late divergence" time scale for the molecular tree of the hominoids; an "early divergence" time scale would make these fossils' placement on the tree correspond to a time about three times their known age. Comparison of limb length on the tree with calculated immunological distances (table on right) shows that the mummy and *Homo erectus* data fit reasonably well, but the *Rama/Siva* data are discrepant with respect to distances to human and chimp. It seems clear, however, that the data do not support a close affinity of *Rama/Siva* and living humans.

albumin, transferrin and DNA data, the best placement of *Rama/Siva* is at the branch point where orang diverges from the line leading to the African apes (Fig. 3). This would fit rather well with Dr. Pilbeam's suggestion that *Sivapithecus* is ancestral to the orang [33]. As the specimens tested were dated at about eight million years, their placement on the molecular tree could provide an independent test of the "molecular clock". It has been suggested that the recent divergence of humans and African apes indicated by molecular similarities is misleading, that there has been a slowdown in the evolution of primate proteins, so that the actual ape-human split could have been fifteen million years ago [2, 8, 18]. If this were the case, the *Rama/Siva* position on the molecular tree would correspond to a time older than fifteen million years; and yet, these specimens known to be about eight million years old do fall on a branch point *deduced* to be eight million years old by the "molecular clock" hypothesis. This tends to support the accuracy of the molecular clock. But I would emphasize that other placements of *Rama/Siva* are statistically possible. This data should be viewed as an example of the way in which fossil proteins can be used to provide information about genetic relations and divergence times; but I consider this particular set of results insufficient for making definitive assertions about the phyletic position of *Ramapithecus/Sivapithecus*.

During the past few years, both the professional journals and the popular media have given prominence to the dispute between Richard Leakey and Donald Johanson about the origins of modern man. Johanson claims that the species he discovered and named, *Australopithecus afarensis*, is ancestral to the later australopithecines, *africanus* and *robustus*, and to the *Homo* lineage [21]. Leakey contends that the australopithecines have nothing to do with the *Homo* lineage, that they represent an evolutionary dead end, and that *Homo* derived from a remote unspecified ancestor [26]. This is another controversy for which fossil proteins might be able to provide evidence in favor of one or the other opposing positions.

In summary, we are living in a time of rapidly increasing information about the evolution of the universe, the evolution of the earth and its continents, and the evolution of the organic molecules which constitute all life on earth. Molecular biology has contributed greatly to our understanding of the genetic and temporal relations of living species. I have described a method for studying fossil proteins which may make it possible to extend the genetic and temporal specificity of molecular data to many of those species which have passed into extinction.

ACKNOWLEDGEMENTS

This work was supported by grants from the Wenner-Gren Foundation, the Leakey Foundation, the National Science Foundation (DEB-8002382), and the University of California, San Francisco. For fossil material I thank Y. Coppens, P.E. Hare, I. Lengyel, D. Pilbeam and B. Vandermeersch. Some sera, antisera, and mammoth and thylacine material were provided by V.M. Sarich, E. Prager and A.C. Wilson. S.L. Washburn and A.L. Zihlman have given invaluable advice and help from the inception of this project. Gary Scheuenstuhl has provided expert technical assistance.

REFERENCES

[1] ARCHER M., *The dasyurid dentition and its relationships to that of didelphids, thylacinids, borhyaenids* (Marsupicarnivora) *and peramelids* (Peramelina: Marsupialia). « Australian J. Zoology », Supp. 39, 1-34 (1976).

[2] AYALA F.J. (ed), *Molecular Evolution.* Sinauer Assoc., Sunderland MA (1976).

[3] BALASZ E.A. (ed.), *Chemistry and Molecular Biology of the Intercellular Matrix*, Vol. 1. Academic Press, New York (1970).

[4] BROWN D.D., *Gene expression in eukaryotes.* « Science », *211*, 667-674 (1981).

[5] CHAMBON P., *Split genes.* « Scientific American », *244*(5), 60-71 (1981).

[6] COLBERT E.H., *Wandering Lands and Animals.* E.P. Dutton, New York (1973).

[7] COPPENS Y., MAGLIO V.J., MADDEN C.T. and BEDEN M., in: *Evolution of African Mammals*, V.J. Maglio and H.B.S. Cooke (eds). Harvard Univ. Press (1978).

[8] CORRUCINI R.S. BABA M., GOODMAN M. *et al.*, *Non-linear macromolecular evolution and the molecular clock.* « Evolution », *34*, 1211-1219 (1980).

[9] CRONIN J.E., BOAZ N.T., STRINGER C.B. and RAK Y., *Tempo and mode in hominid evolution.* « Nature », *292*, 113-122 (1981).

[10] CRONIN J.E. and SARICH V.M., *South American molecular systematics, evolutionary clocks, and continental drift.* In: « Origin of the New World Monkeys and Continental Drift ». Chiarelli and Ciochon R. (eds.). Academic Press, New York (1981).

[11] DAYHOFF M.O., *Atlas of Protein Sequences and Structure*, Vol. 5, Supp. 3. National Biomedical Research Foundation, Washington D.C. (1978).

[12] DICKERSON R.E., *The structure of cytochrome c and the rates of molecular evolution.* « J. Molecular Evol. », *1*, 26-45 (1971).

[13] DICKERSON R.E., *The structure and function of an ancient protein.* « Scientific American », *226*(4), 58-72 (1972).

[14] DOOLITTLE R.F., SCHUBERT O. and SCHWARTZ S.A., *Amino acid sequence studies on artiodactyl fibrinopeptides I.* « Arch. Bioch. Biophys », *118*, 456-467 (1967).

[15] DOOLITTLE W.F. and SAPIENZA C., *Selfish genes, the phenotype paradigm and genome evolution.* « Nature », *284*, 601-607 (1980).

[16] FIETZEK P.P. and KUHN K., *The primary structure of collagen.* « Int. Rev. Connective Tissue Res. », *7*, 1-60 (1976).

[17] FURTHMAYR H. and TIMPL R., *Immunochemistry of collagens and procollagens.* « Int. Rev. Connective Tissue Res. », *7*, 61-101 (1976).

[18] GOODMAN M. and TASHIAN R. (eds.), *Molecular Anthropology.* Plenum, New York (1976).

[19] HEDGES R.E.M., *Radioisotope clocks in archeology.* « Nature », *281*, 19-24 (1979).

[20] JACOBS L.L. and PILBEAM D., *Of mice and men: fossil-based divergence dates and molecular "clocks".* « J. Human Evol. », *9*, 551-555 (1980).

[21] JOHANSON D.L. and EDEY M., *Lucy.* Simon and Schuster, New York (1981).

[22] JUKES T.H., *Silent nucleotide substitutions and the molecular evolutionary clock.* « Science », *210*, 973-978 (1980).

[23] KIMURA M., *The neutral theory of molecular evolution.* « Scientific American », *241*(5), 98-126 (1979).

[24] KIMURA M., *A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences.* « J. Molecular Evol. », *16*, 111-120 (1980).

[25] KING M.-C. and WILSON A.C., *Evolution at two levels in humans and chimpanzees.* « Science », *188*, 107-116 (1975).

[26] LEAKEY R.E.F., *The Making of Mankind.* E.P. Dutton, New York (1981).

[27] LI W.-H., GOJOBORI T. and NEI M., *Pseudogenes as a paradigm of neutral evolution.* « Nature », *292*, 237-239 (1979).

[28] LOWENSTEIN J.M., *Immunospecificity of fossil collagens.* In: « Biogeochemistry of Amino Acids », Hare P.E. (ed.). John Wiley, New York (1980).

[29] LOWENSTEIN J.M., *Species-specific proteins in fossils.* « Naturwissenschaften », *67*, 343-346 (1980).

[30] LOWENSTEIN J.M., SARICH V.M. and RICHARDON B.J., *Albumin systematics of the extinct mammoth and Tasmanian wolf.* « Nature », *291*, 409-411 (1981).

[31] LOWENSTEIN J.M., *Immunological reactions from fossil material.* « Phil. Trans. Royal Soc. London », B*292*, 143-149 (1981).

[32] ORGEL L.E. and CRICK F.H.C., *Selfish DNA: the ultimate parasite.* « Nature », *284*, 604-607 (1980).

[33] PILBEAM D., *New hominoid skull material from the Miocene of Pakistan.* « Nature », *295*, 232-234 (1982).

[34] PRAGER E.M., WILSON A.C., LOWENSTEIN J.M. and SARICH V.M., *Mammoth albumin.* « Science », *209*, 287-289 (1980).

[35] SARICH V.M. and WILSON A.C., *Immunological time scale for hominid evolution.* « Science », *158*, 377-387 (1972).

[36] SARICH V.M. and CRONIN J.E., *Molecular systematics of the primates.* In: Ref. 18.

[37] SCHOPF T.J.M., RAUP D.M., GOULD S.J. *et al.*, *Genomic versus morphological rates of evolution: influence of morphologic complexity.* « Paleobiology », *1*, 63-70 (1975).

[38] SIBLEY C.G. and AHLQUIST J.E., *The relationships of the yellow-breasted chat* (Icteria virens) *and the alleged slowdown in the rate of macromolecular evolution in birds.* « Postilla No. », *187*, 1-19 (1982).

[39] SILK J., *The Big Bang.* W.H. Freeman, San Francisco (1980).

[40] SIMONS E.L., *Ramapithecus.* « Scientific American », *236*(5), 28-35 (1977).

[41] SOLOMON E. and CHEAH K.S.E., *Collagen evolution.* « Nature », *291*, 450-451 (1981).

[42] WATSON J., *The Double Helix.* New American Library, New York (1968).

[43] WILSON A.C., CARLSON S.S. and WHITE T.J., *Biochemical evolution.* « Ann. Rev. Biochem », *46*, 573-639 (1977).

[44] WILSON J.T. (ed.),*Continents Adrift.* W.H. Freeman, San Francisco (1973).

[45] WYCKOFF R.W.G., *The Biochemistry of Animal Fossils.* Williams and Wilkins, Baltimore (1972).

[46] YAMADA K.Y. and OLDEN K., *Fibronectins - adhesive glycoproteins of cell surface and blood.* « Nature », *275*, 179-184 (1978).

[47] ZIHLMAN A.L. and LOWENSTEIN J.M., *False start of the human parade.* « Natural History », *88*(7), 86-91 (1979).

[48] ROMER A.E., *Vertebrate Paleontology.* U. of Chicago Press (1971).

LES CHROMOSOMES ET L'ESPECE

JÉRÔME LEJEUNE
Académicien Pontifical

SUMMARY. — Living beings are separated into various species, the boundaries of which are defined by the sterility of the hybrids (for example, the mule born from a mare and a donkey).

The simplified aphorism: "one species, one karyotype" exemplifies the situation. It is the chromosomal disparities which prevent a correct meïosis in the hybrid. Hence in the course of chromosomal changes (Species evolution) every novelty must be put at the homozygous stage to perpetuate effectively. Only the highest consanguinity can speed this process enough. At the extreme, autofecundation is very expedient as demonstrated in vegetals.

In higher animals a rare mechanism (monozygous heterokaryotic twinning), very close to autofecundation, can produce at once a male and a female, carriers of a chromosomal rarity at the homozygous stage.

These reflexions on chromosomal mechanisms show that a population cannot evolve as a whole from one species-type to another one. On the contrary, each new species must emerge from a very small stem, eventually as restricted as a unique couple.

A secondary genic divergence (genetic by mutation and selection) will produce races inside the chromosomally defined species. But chromosomal rearrangements are possibly more than a purely reproductive barrier. As exemplified recently in various tumor cells (leukoemias, lymphomas) the transposition of some genes to another location can modify enormously their expression, and change drastically the phenotype.

Moreover, it is an open possibility that chromosomal rearrangements do not occur at random. Some of them could very well be favored by the very functioning of the genes close to the breaking points.

These considerations lead to the conclusion that the speciation process by chromosomal changes could have an inner logic which remains to be discovered.

Que les êtres vivants soient cantonnés chacun dans son espèce, mérite considération. Telle qu'elle est formulée aujourd'hui la théorie synthétique de l'évolution s'accommoderait fort bien d'une sorte de continuum génétique, du protiste à l'éléphant: pour peu qu'ils survinssent entre formes assez proches, tous les croisements intermédiaires seraient a priori possibles et partiellement fertiles, permettant de parcourir tout l'éventail taxinomique par hybridations successives judicieusement menées.

Le fait est qu'il n'en est rien.

Reste alors à se demander si le cloisonnement en espèces distinctes est une étape nécessaire à toute évolution; la mécanique chromosomique incline à supposer que oui.

La barrière génétique entre espèces

Un exemple familier, celui de l'âne et du cheval, permet de définir cette barrière génétique.

Le mulet, né d'une jument et d'un baudet, ou le bardot, né d'une ânesse et d'un étalon, sont fort bien conformés et, pour certaines qualités, supérieurs à leurs parents: la sobriété de la mule et la sureté de son pas ont fait largement leurs preuves.

Les différences géniques entre l'âne et le cheval n'entrainent donc aucune incompatibilité et ne constituent pas une barrière. Mais ces hybrides sont stériles: mule, mulet, bardot, bardote, ne peuvent engendrer ni entre eux ni avec les espèces parentales. Cette stérilité, cette impossibilité de faire passer un gène d'âne chez les chevaux crée justement la barrière entre les deux espèces. Si le flux génique était possible de l'une à l'autre, il n'y aurait que des « chevânes » et non des ânes et des chevaux.

Avec les méthodes modernes [1] on décèle des différences de structure chromosomique ajoutées à la différence de nombre (62 chez l'âne, 64 chez le cheval) et on reconnait côte à côte chez l'hybride les chromosomes de l'âne et ceux du cheval. Les éléments qui ne sont ni de même nombre ni de même forme ne peuvent s'apparier deux à deux au moment de la maturation des cellules reproductrices: Il en résulte, soit un blocage des divisions cellulaires, soit une production de gamètes tellement déséquilibrée, qu'ils ne peuvent donner naissance à un être viable.

Ce même type de différences chromosomiques entre espèces proches parentes a été retrouvé dans tout l'éventail des prosimiens, des simiens et des primates comme l'a démontré Bernard Dutrillaux. Dès lors, en pendant de l'aphorisme « un gène - un enzyme », qui permit de fonder la Biologie moléculaire: il devient possible [2] de fonder la taxinomie chromosomique sur l'aphorisme « une espèce - un caryotype ». Les différences entre gènes définissent les races, les différences entre chromosomes bornent les espèces.

Une espèce - un caryotype

Les remaniements chromosomiques séparant les quatre grandes espèces, orang outan, gorille, chimpanzé et homo sapiens, sont maintenant bien définis (cf. B. Dutrillaux). Au moins douze à quinze changements majeurs ont été nécessaires pour passer d'un éventuel ancêtre commun aux formes actuelles.

Ce fait oblige à revoir l'idée d'une évolution progressive, modifiant insensiblement une population entière au cours de milliers d'années. De même il devient improbable qu'une convergence fortuite entre populations différentes ait conduit à l'uniformité actuelle du caryotype humain (vérifiée sur des centaines de milliers d'individus, du bochiman au patagon et du scandinave à l'aborigène d'Australie) [3]. Force est de considérer que les représentants des grandes espèces actuelles descendent tous d'un rameau extrêmement petit, propre à chacune d'elle.

Les remaniements chromosomiques

La pathologie chromosomique est une exception apparente à cette homogénéité de l'espèce: certains malades portent un chromosome en trop (trisomie 21 appelée autrefois mongolisme) ou un segment en moins (maladie du cri du chat par perte du bras court du cinq) ou encore des remaniements plus complexes. Mais chaque fois qu'on observe un excès ou un manque d'un segment chromosomique il en résulte une maladie grave interdisant à cette nouveauté de faire souche.

Même les remaniements de structure ne s'accompagnant pas d'un déséquilibre génique, sont défavorables puisqu'ils réduisent, toujours, et parfois totalement, la fertilité du sujet portant côte à côte la structure ancienne et la structure nouvelle [2].

La sélection naturelle tend donc à éliminer les nouveautés chromosomiques, d'où la stabilité apparente du caryotype des espèces.

Certes, des espèces très voisines peuvent ne différer que par un seul remaniement équilibré entre deux chromosomes, tels Equus Caballus et Equus przewalsky [4], mais même dans ce cas les hybrides souffrent d'une réduction de la fertilité.

Il en résulte que chacune des étapes ayant permis de passer d'une espèce ancestrale aux espèces actuelles, a dû se réaliser en dépit d'une sélection naturelle sévère.

Pour doubler ce cap difficile, il est nécessaire que surviennent des individus porteurs de la nouveauté en double exemplaire (homozygotes). Les deux éléments remaniés peuvent alors s'apparier normalement ce qui rétablit la fertilité. En appliquant les équations habituelles de la génétique des populations on démontre aisément que le groupe de reproducteurs dans lequel apparaît la nouveauté doit être aussi restreint que possible pour que des sujets homozygotes aient quelque chance d'apparaître et de fonder une nouvelle lignée.

Cette consanguinité nécessaire amène à considérer que l'autofécondation serait le moyen le plus expédient. C'est d'ailleurs ce qu'on observe chez les plantes et le *Raphano brassica*, hybride de radis et choux obtenu par Karpechenko [4] l'a été de cette manière. Aucune espèce nouvelle n'a été obtenue, même chez les plantes, par sélection massale portant sur toute une population.

La spéciation d'emblée

Comme l'autofécondation n'existe pas chez les mammifères, il est évident que cette voie, la plus simple possible n'a pas été choisie au cours au l'évolution. Mais la pathologie humaine nous fournit un modèle extrêmement proche de l'autofécondation [5].

On sait que les jumeaux identiques sont issus du clivage d'un seul oeuf en deux embryons distincts.

A partir d'un oeuf XY, il arrive exceptionnellement que le chromosome Y soit perdu lors de la séparation. Il en résulte deux jumeaux monozygotes hétérocaryotes [6]. L'un d'eux persiste dans son devenir de garçon, l'autre qui n'a pas reçu de chromosome Y, se développe en une femme imparfaite (Syndrome de Turner).

Trois observations de ce type de gemellité monozygote hétérocaryote sont actuellement connus [7].

Dans notre espèce, le syndrome de Turner détermine une aplasie des ovaires et donc une stérilité, ce qui paraît un handicap difficilement acceptable pour l'établissement d'une espèce nouvelle.

Mais, chez la souris par exemple, la femelle à un seul X (équivalent du syndrome de Turner) est viable et féconde. Chez cet animal, il est théoriquement parfaitement possible de partir d'un oeuf mâle, d'en tirer une femelle, qui est très précisément issue d'un fragment de son frère, et de croiser ensuite entre eux ces deux jumeaux, réalisant ainsi, génétiquement parlant, l'équivalent d'une autofécondation.

Cette manipulation n'a pas encore été réalisée, mais, jointe à la production d'un remaniement chromosomique cloisonnant, du type de ceux que nous avons discutés précédemment, elle constituerait une méthode de spéciation d'emblée par couple unique.

L'émergence d'une espèce

Quel que soit le processus réellement employé par la nature, consanguinité très étroite pendant quelques générations ou spéciation par couple unique en une seule génération, les lois de la mécanique chromosomique imposent absolument qu'une espèce nouvelle apparaisse sur un rameau extrêmement petit qui se détache presque immédiatement de la souche.

Autrement dit, l'hypothèse néo-darwinienne classique d'une accumulation insensible de petits changements géniques (mutations ponctuelles) faisant évoluer très lentement toute une population vers un type nouveau est définitivement exclue.

A partir d'un ancêtre commun dont nous pouvons à peu près reconstituer le caryotype (Dutrillaux), il ne peut pas s'être produit une chimpanzification continue, une gorillisation insensible, une orangoutanisation imperceptible ou encore une hominisation lentement progressive.

Bien au contraire, il est nécessaire de postuler des changements brusques, quasi instantanés à l'échelle géologique, faisant apparaître, chromosome nouveau, par chromosome nouveau, des espèces d'emblée distinctes et d'emblée divergentes.

Un tel processus par saut brusque, déjà postulé par Goldschmidt [8], est d'ailleurs en stricte concordance avec la paléontologie. Un nombre élevé d'espèces distinctes, marque incontestablement l'évolution des primates, et en aucun cas le glissement néo-darwinien n'est en accord avec les faits.

Il serait présomptueux d'étendre ces conclusions à l'ensemble du règne vivant car nos connaissances cytogénétiques de la structure fine des chromosomes sont actuellement limitées à un très petit nombre d'espèces. Toutefois il semble qu'un modèle de ce genre soit applicable à l'ensemble des Mammifères.

La divergence des espèces

Reste a trancher la question cruciale: les remaniements chromosomiques ont-ils seulement un effet cloisonnant? ou bien jouent-ils aussi un rôle dans la divergence?

Si l'effet cloisonnant était seul en jeu, la divergence morphologique et fonctionnelle qui fait reconnaître d'un coup d'oeil un cheval d'un âne ou un homme d'un chimpanzé résulterait exclusivement de l'accumulation de mutations gèniques dans des populations séparées l'une de l'autre par une barrière génétique. Ces mutations pourraient être purement fortuites (mutations neutres de Kimana [9] ou bien être secondairement triées par la sélection naturelle (hypothèse néo-darwinienne classique).

Dans ces conditions, la spéciation chromosomique jouerait un rôle comparable à celui de la simple séparation géographique. Or, cette dernière ne parvient pas semble-t-il à fabriquer autre chose que des races variées à l'intérieur d'une espèce, comme le montre d'abondance, le morcellement des populations humaines sur le globe.

Il paraît donc nécessaire d'envisager aussi que certains remaniements chromosomiques puissent modifier l'expression des gènes, soit à l'état hétérozygote (changement primitif), soit après passage à l'homozygotie (espèce émergence).

L'exemple de plusieurs maladies médullo-sanguines montre qu'un effet hétérozygote est possible. Ainsi la translocation réciproque d'un fragment du 22 sur le bras long du 9 est caractéristique de la leucémie myeloïde chronique (Rowley [10]), celle du bras long du 8 sur le bras long du 21 se rencontre dans la leucémie myéloblastique aiguë, tandis qu'un échange entre les bras longs du 15 et du 17 est typique de la leucémie aiguë à promyélocytes [10].

De même dans les lignées du genre lymphome de Burkitt avec expression anormale des immunoglobulines, le remaniement atteint toujours la même zone d'un chromosome 8. Si le segment transféré à cet endroit provient d'un 2, les chaînes Kappa sont exprimées; si le segment provient d'un 22, les chaînes Lambda sont exprimées. Enfin si le segment provient d'un 14, les deux types Kappa et Lambda sont exprimés. (Leloir *et coll.* [11]).

Autant qu'on puisse le savoir les gènes situés sur le 2, le 22, le 14, restent eux-mêmes inchangés; seule leur expression est modifiée.

L'ensemble de ces faits permet d'affirmer, qu'au niveau cellulaire tout au moins, certains déplacements de gènes modifie grandement leur effet. Ceci rappelle de très près le classique effet de position bien connu chez les végétaux ou chez la drosophile (voir [2] pour référence).

Par ailleurs il se pourrait que les remaniements chromosomiques ne soient pas strictement fortuits. Il est clair que dans l'ataxie télangiectasique, les remaniements survenant dans les lymphocytes intéressent des points spécifiques, toujours les mêmes, du chromosome 7 et du chromosome 14 (Aurias [12]). D'où la notion qu'une mutation génique, celle qui provoque la maladie, pourrait fragiliser électivement certains sites chromosomiques et favoriser les remaniements à leur niveau.

Par ailleurs, ainsi que l'ont remarqué Dutrillaux *et coll.* [13], certains accidents, spontanés ou radio-induits produisent chez l'homme des remaniements qui reconstituent un chromosome « ancestral » ou encore une structure chromosomique aujourd'hui normale dans une autre espèce.

De plus les types de remaniements varient très nettement d'un groupe à l'autre: les translocations dominent chez les lémurs, les fissions chez les cercopithèques et les inversions chez les pongidés (Dutrillaux *et coll.* [13]. Il est donc possible que certains remaniements soient plus probables que d'autres et que la structure du caryotype ou du génome modifie cette probabilité.

Il se pourrait alors que les spéciations successives aient accumulé les remaniements qui étaient à la fois les plus probables à l'époque et les plus aptes à régler harmonieusement l'expression des gènes (voir Lejeune [2] pour discussion).

Conclusion

Cette brève analyse ne prétend nullement mettre fin à la discussion entre tenants des mutations géniques d'une part, et partisans des remaniements chromosomiques de l'autre. Il est tout à fait certain que les deux phénomènes ont une importance considérable.

Trois conclusions provisoires sont toutefois intéressantes:

— L'évolution du caryotype des primates permet d'affirmer que la théorie purement mutationnelle (néo darwinisme strict) est insuffisante. Elle s'applique bien aux races, elle n'explique nullement les espèces.

— Les remaniements chromosomiques sont caractéristiques de la spéciation dont ils représentent probablement le mécanisme majeur; d'où l'apparition de chaque espèce nouvelle sur un rameau extrêmement ténu.

— La survenue de tel ou tel remaniement peut être favorisée ou interdite par l'état actuel du caryotype ou du génome.

En définitive il se pourrait fort bien que selon des lois qui restent à découvrir, l'évolution des espèces se conforme à une logique que nous ne connaissons pas encore. Ainsi s'expliquerait le fait que les « trouvailles » de l'évolution aient permis l'émergence de qualités exceptionnelles, (telle l'intelligence réfléchie de l'homme) que le hasard seul, même trié par la sélection naturelle, eût été tout à fait incapable de produire.

REFERENCES

[1] BIEMONT CL. et LAURENT C., « C.R. Acad. Sci. (Paris) », *279*, Série D, 323-326 (1974).

[2] LEJEUNE J., « C.R. Soc. Biol. (Paris) », *169*, 828-844 (1975).

[3] Données personnelles de l'Istitut de Progenèse.

[4] KARPECHENKO L., « Zeitschr. ind. Abstamm. Vererbungsl. », *39*, 1-7 (1928).

[5] LEJEUNE J., « Nouv. Rev. Théol. », *90*, 191 (1968).

[6] TURPIN R., LEJEUNE J., LAFOURCADE J., CHIGOT P.L. et SALMON C., « C.R. Acad. Sci. (Paris) », *252*, 2945-2946 (1961).

[7] AURIAS A., *Contribution à l'étude du mécanisme et de la signification du monozygotisme hétérocaryote.* Thèse de Médecine, Paris (1974).

[8] GOLDSCHMIDT R., « L. Zeitschr. ind. Abstamm. Vererbungs. », *39*, 1-7 (1928).

[9] KIMURA M., *La théorie neutraliste de l'évolution moléculaire.* « Pour la Science (Scientific American) », *27*, 48 (1980).

[10] ROWLEY J.D., « Ann. Rev. Genet. », *14*, 17-39 (1980).

[11] LELOIR G., PREUD'HOMME J.L., BERNHEIM A. et BERGER R., « C.R. Acad. Sci. Paris », *293*, III, 427-429 (19 ?).

[12] AURIAS A., « J. Génét. Hum. », *29*, 235-247 (1981).

[13] DUTRILLAUX B., COUTURIER J., VIEGAS-PEQUIGNOT E., CHAUVIER G. et TREBBAU P., « Ann. Genet. », *21*, 142-148 (1978)

[14] DUTRILLAUX B., COUTURIER J. et VIEGAS-PEQUIGNOT E., *Chromosomes today.* Vol. 7, pp. 176-191. George Allen et Unwin edit. (1981).

APPROCHE CYTOGENETIQUE DE LA POSITION PHYLETIQUE DE L'HOMME

BERNARD DUTRILLAUX
Maître de Recherches au CNRS
Institut de Progenèse
Paris

SUMMARY. — Comparative cytogenetics has encountered a new interest with the development of a series of chromosome banding techniques, making possible more and more accurate comparisons. It could be shown that the chromosome bands, corresponding to about 1000 structures, are almost, and perhaps entirely, identical in many primate species. This conclusion will probably be extended to other eutherian mammals, at present under study. The very numerous chromosome similarities from more and more distantly related species led us to propose a reconstitution of the ancestral aspect of the karyotype of the eutherian mammals. From this starting point, the mutations affecting the chromosomes could be reconstructed, and the information could be used for establishing the phylogeny of the primates. The place of man in relation to the other primates can be proposed as follows: most of the evolution of man's ancestors was also common to chimpanzee, gorilla and orang-utan. Chimpanzee appears as our closest relative, and gorilla is also very close. Orang-utan is more distantly related, and can be considered, for many parameters, as near to the common ancestor of man, gorilla and chimpanzee. The Hominidae, the family to which man belongs, was derived from Pongidae, the family to which chimpanzee, gorilla and orang-utan belong.

Considered in their whole, the chromosomal mutations did not occur at random since the various types (translocations, inversions, fissions) are distributed very differently from one family to another. Furthermore, considering the chromosomal changes detected in actual human populations, or experimentally induced in human cells, many reproduce ape or monkey chromosomes (reverse or convergent mutations), giving another demonstration on the non-random process of chromosomal rearrangements.

Moyens d'étude actuels des chromosomes

Depuis la découverte des bandes chromosomiques, au début des années 70, les techniques d'analyse n'ont cessé de se multiplier et de s'améliorer. Leur pouvoir de résolution a triplé en 10 ans et un millier de bandes sont maintenant décelables par caryotype haploïde.

Bien qu'elle soit d'une toute autre nature, cette information approche celle fournie par l'étude des chromosomes géants de la Drosophile, qui ont

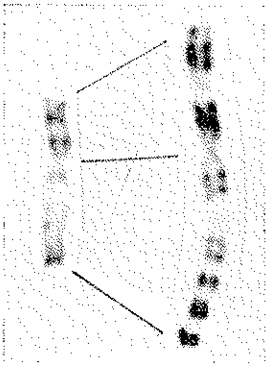


FIG. 1. Chromosomes X humains en bandes R. A gauche: marquage classique, à droite: marquage après incorporation de 5-bromodéoxyuridine et synchronisation des cultures.

pendant longtemps fait de cet animal le matériel de prédilection de la génétique.

La figure 1 montre un chromosome X humain tel qu'on le voyait il y a une dizaine d'années et tel qu'on peut l'observer maintenant.

Les principaux artifices employés pour faire apparaître un maximum de structures sont la culture cellulaire suivie d'une synchronisation. Cette dernière permet de ne plus utiliser la colchicine, intéressante pour accumuler les mitoses, mais qui avait l'inconvénient d'entraîner une forte condensation chromosomique.

Un autre artifice consiste à faire incorporer dans l'ADN en réplication un précurseur comme la 5-bromodéoxyuridine qui modifie la condensation des segments chromosomiques l'ayant incorporé.

Ces méthodes permettent aussi d'étudier la dynamique de la réplication de l'ADN, et de caractériser chaque bande par son temps de réplication.

Ainsi, chacune des 1000 petites bandes du caryotype peut-être définie comme un segment d'ADN et de protéines où se trouvent localisés quelques dizaines de gènes, soumis à un même système de régulation chromosomique. S'il ne s'agit peut-être pas encore du niveau moléculaire de l'opéron et du réplicon, il est évident que les distances qui semblaient naguère infranchissables entre la cytogénétique et la biologie moléculaire se sont considérablement réduites.

Les méthodes d'hybridation moléculaire d'ADN ou d'ARN radioactif de synthèse, directement sur l'ADN chromosomique, permettent d'ailleurs de connaître la composition moléculaire exacte de certains segments chromosomiques entiers.

Enfin, dernier appoint à l'analyse chromosomique, la cartographie génique apporte un autre élément d'importance. Par différentes méthodes, les gènes peuvent être assignés à des chromosomes, voire même précisément localisés sur une bande chromosomique. Par les études comparées, on peut conclure que les mêmes bandes, telles que nous les avons définies plus haut, portent les mêmes gènes, d'une cellule à l'autre, d'un individu à l'autre et même d'une espèce à l'autre. Ceci confirme l'une des leçons enseignées par la cytogénétique comparée: le matériel génétique est resté d'une très grande stabilité au cours de l'évolution.

Cette extraordinaire stabilité fait que chaque chromosome n'a subi que peu de modifications, au cours de la centaine de millions d'années recouvrant l'histoire des primates. Les chromosomes peuvent donc être comparés, d'une espèce à l'autre, et la reconstitution de leurs quelques modifications permet de situer les espèces les unes par rapport aux autres et finalement de mieux comprendre leur phylogénie.

Comparaisons interspécifiques du caryotype

Malgré les variations interspécifiques existant parfois, il est généralement possible de standardiser le caryotype d'une espèce ou d'une sous-espèce donnée, ce qui est fait chez l'homme, par exemple, depuis de nombreuses années. De là, il est possible de comparer les caryotypes d'espèces proches, et nous prendrons comme exemple la comparaison homme-chimpanzé.

La figure 2 montre une telle comparaison, après marquage en bandes R. Il est clair que de nombreux chromosomes sont similaires: les 3, 6, 7, 8, 10, 11, 14, 16, 19, 20, 21, 22 et X. Il est assez facile de comprendre les changements séparant les autres chromosomes car il s'agit surtout de remaniements ne touchant qu'un seul chromosome à la fois (intrachromosomiques). Ainsi, les 5, 12, 15, 17, et 18 ne diffèrent que par une inversion péricentrique. Les chromosomes 4 et 9 diffèrent par 2 inversions. Le chromosome 1 humain porte plus d'hétérochromatine et le 13 de chimpanzé possède 2 bandes en plus.

Enfin, le 2 humain est formé de la fusion de 2 chromosomes présents chez le chimpanzé.

Ainsi, la comparaison chromosomique, homme-chimpanzé montre la proximité des espèces. Leurs chromosomes diffèrent peu, mais cette seule étude ne permet aucune conclusion d'ordre phylogénique. En particulier,

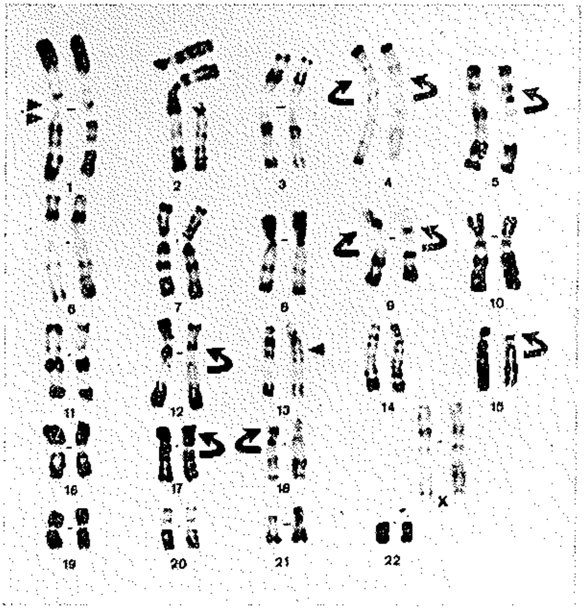


FIG. 2. Comparaison d'un demi-caryotype d'homme (à gauche pour chaque paire) et d'un demi-caryotype de chimpanzé (à droite). Ils diffèrent par 9 inversions péricentriques (flèches courbes), une fusion (flèche droite) et une addition de matériel sur le 1 humain et le 13 de chimpanzé (triangles noirs).

il est impossible d'en déduire si un chromosome est éventuellement ancestral par rapport à l'autre.

Cette étape ne peut être franchie que par les comparaisons croisées de plusieurs espèces, ce que nous allons aborder maintenant.

Etablissement de la phylogénie « chromosomique » des primates

Si l'on ajoute à la comparaison homme-chimpanzé celle d'un plus grand nombre d'espèces, d'autres modifications chromosomiques vont apparaître. Particulièrement informatives sont les modifications d'un même chromosome chez plusieurs espèces, car elle peut amener à déduire l'ordre dans lequel les remaniements sont survenus.

Ainsi, la figure 3 montre les divers aspects des composants du chromosome 1 humain chez quelques primates sélectionnés. Il est certain qu'une telle reconstitution n'a de valeur que si elle est faite pour tous les chromosomes, et que s'il n'existe aucune contradiction en considérant tous les éléments ensemble. Ces deux conditions ont été remplies.

A titre d'exemple, nous allons donc détailler cette évolution du chromosome 1 humain.

Chez certains prosimiens, il existe un grand chromosome à centromère distal (acrocentrique), dont le marquage ressemble beaucoup à celui du bras court du chromosome 1 humain. Le reste du chromosome 1 humain ne se reconnait pas aisément et correspond probablement à deux ou plusieurs microchromosomes.

Chez de nombreux platyrhiniens, ou singes du nouveau monde, on retrouve le grand acrocentrique, et en plus, un autre acrocentrique correspondant imparfaitement au bras long du chromosome 1 humain (CCA et ATR sur la figure 4).

Chez la plupart des catarhiniens, ou singes de l'ancien monde, un grand chromosome, assez semblable au 1 humain est observé. Toutefois.

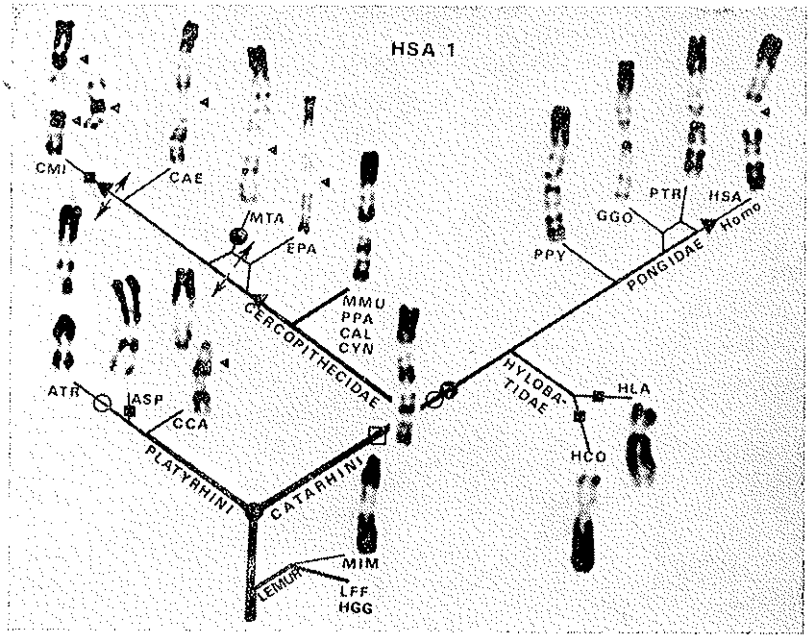


FIG. 3. Evolution des chromosomes équivalents au 1 humain. Les noms d'espèces sont schématisés par des codes à 3 lettres dont l'explication est donnée avec la figure 5. Cercle blanc = inversion péricentrique, autres cercles = autres inversions, carré blanc = fusion, carré noir = translocation entre 2 chromosomes, triangle noir = modification de l'hétérochromatine.

des différences de détails sont décelables. Chez les cercopithécoïdes (MMU, EPA etc... de la figure 4), le bras le plus long est très semblable au grand acrocentrique dont nous parlions plus haut et le bras le plus court à l'autre acrocentrique des platyrhiniens. On peut donc conclure qu'une fusion des 2 acrocentriques est survenue pour donner le grand élément.

Chez les Pongidae, ce grand élément possède un centromère plus médian, son bras long étant raccourci et son bras court allongé. Une inversion d'un court segment, autour du centromère (inversion péricentrique) est responsable de ce changement. Par ailleurs, la séquence des bandes du bras

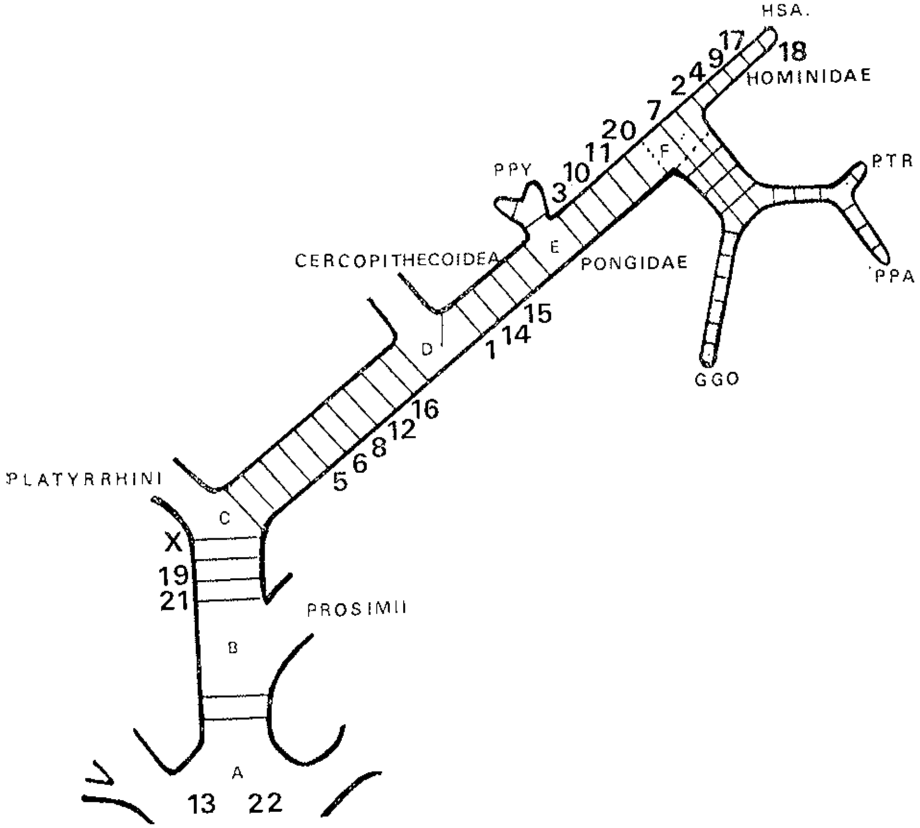


Fig. 4. Arbre montrant l'évolution chromosomique vers les Pongidae et l'homme. HSA = *H. sapiens*; PTR = *P. troglodytes*; PPA = *P. paniscus*; GGO = *G. gorilla*; PPY = *P. pygmaeus*. Chaque trait représente un remaniement chromosomique. Les numéros indiquent, entre chaque bifurcation, la formation des chromosomes humains sous leur forme actuelle, ce qui permet d'une certaine façon, de les dater.

qui a été allongé est changée. Une autre inversion, n'intéressant pas le centromère (inversion paracentrique) en est responsable.

Finalement, l'adjonction d'hétérochromatine donne au chromosome 1 humain son aspect actuel. Sans vouloir entrer dans le détail de tous les remaniements subis par ce chromosome, on peut cependant mettre en évidence la survenue d'une séquence d'évènements, allant des prosimiens, passant par les platyrhiniens, puis les cercopithécoïdes, et les Pongidae, avant d'arriver à l'homme.

Il serait fastidieux de faire une description de tous les remaniements affectant tous les chromosomes. Ceci a déjà été rapporté dans un certain détail [1]. On comprendra cependant que l'accumulation des données fournies par chaque remaniement de chaque chromosome constitue une information très riche, permettant de situer les uns par rapport aux autres les espèces, les genres, les familles etc...

Les figures 4 et 5 montrent des résumés de cette information qui permet donc de construire l'arbre généalogique des primates, en se basant exclusivement sur l'étude cytogénétique de près d'une centaine d'espèces, c'est-à-dire sur environ la moitié des espèces existantes. Nous reviendrons plus loin sur les implications de ces résultats sur la phylogénie directe de l'homme.

Reconstitution de caryotypes ancestraux et datation des chromosomes

Dans le précédent paragraphe, nous avons utilisé les différences chromosomiques pour établir une phylogénie des espèces. Les comparaisons chromosomiques mettent aussi en lumière l'existence de chromosomes identiques chez 2 ou plusieurs espèces, ce qui implique immédiatement que les ancêtres communs à ces espèces possèdaient eux-mêmes déjà, très probablement, ces chromosomes. Par exemple, si l'on reprend la comparaison homme-chimpanzé de la figure 2, on peut conclure que leurs derniers ancêtres possédaient déjà les mêmes chromosomes 3, 6, 7, 8, 10, 11, 14, 16, 19, 20, 21, 22 et X. Si l'on ajoute la comparaison d'une troisième espèce comme l'orang-outang, un certain nombre de ces chromosomes seront modifiés, parce qu'ils ont subi une mutation soit dans la branche commune homme-chimpanzé, soit dans le rameau menant à l'orang-outang. Inversement, d'autres chromosomes apparaîtront identiques chez l'homme et l'orang-outang, comme par exemple, les chromosomes 5 et 12, parce qu'ils ont muté dans le rameau menant au chimpanzé. Les mêmes chromosomes 5 et

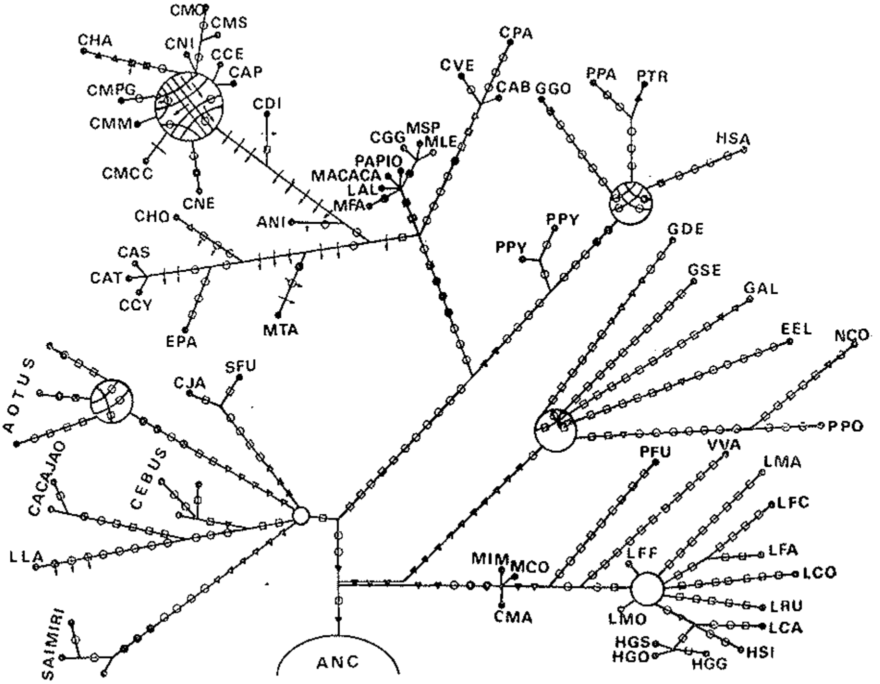


FIG. 5. Autre représentation de l'évolution chromosomique à l'échelle de tous les primates étudiés. Chaque type de remaniement a été symbolisé. Flèche = fission, carré blanc = translocation Robertsonienne, carré noir = autre translocation, rond blanc = inversion péricentrique, rond noir = autre remaniement intra-chromosomique. Noter la forte concentration d'un même type de remaniement sur différentes branches. Les noms d'espèces sont indiqués par des codes à 3 lettres:

PROSIMII — *Lemuridae*:

MIM : *Microcebus murinus*; MCO : *Microcebus coquereli*; CMA : *Cheirogaleus major*; PFU : *Phaner furcifer*; VVA : *Varecia variegata*; LLF : *Lemur fulvus fulvus*; LFA : *L. fulvus albocollaris*; LFC : *L. fulvus collaris*; LMO : *L. mongoz*; LMA : *L. macaco*; LCO : *L. coronatus*; LRU : *L. rubriventer*; LCA : *L. catta*; HSI : *Hapalemur simus*; HGG : *H. griseus griseus*; HGO : *H. griseus occidentalis*; HGS : *H. griseus subspecies.*

— *Galagidae*:

GDE : *Galago demidovii*; GAL : *G. alleni*; GSE : *G. senegalensis*; EEL : *Euoticus elegantulus.*

— *Lorisidae*:

NCO : *Nycticebus coucang*; PPO : *Perodycticus potto.*

SIMII — *Cebidae*:

LLA : *Lagothrix lagotricha.*

— *Callitricidae*:

SFU : *Saguinus fuscicollis*; CJA : *Callithrix jacchus.*

— *Cercopithecidae*:

MTA : *Miopithecus talapoin*; EPA : *Erythrocebus patas*; ANI : *Allenopithecus nigroviridis*; CCY : *Cercopithecus cynosurus*; CAT : *C. aethiops tantalus*; CSA : *C. sabaeus*; CHO : *C. l'hoesti*; CDI : *C. diana*; CAP : *C. ascanius petaurista*; CCE : *C. cephus*; CMS : *C. mitis stuhlmanni*; CMO : *C. mitis opisthosticus*; CNI : *C. nictitans*; CHA : *C. hamlyni*; CMPG : *C. (mona) pogonias grayi*; CMM : *C. (mona) mona*; CMCC : *C. (mona) campbelli campbelli*; CNE : *C. neglectus*; MFA : *Macaca fascicularis*; MMU : *M. mulatta*; MMA : *M. maura*; MNI : *M. nigra*; MSY : *M. sylvana*; PAP : *Papio papio*; PAN : *P. anubis*; PHA : *P. hamadryas*; PCY : *P. cynocephalus*; PPR : *P. porcarius*; LAL : *Lophocebus albigena*; LAT : L. aterrimus; CTF : *Cercocebus torquatus fuliginosus*; CTT : *Cercocebus torquatus torquatus*; CGG : *C. galeritus galeritus*; CGC : *C. galeritus chrysogaster*; MLE : *Mandrillus leucophaeus*; MSP : *M. sphinx.*

— *Colobidae*:

CVE : *Colobus vellerosus*; CPA : *C. palliatus*; CAB : *C. abyssinicus.*

— *Pongidae*:

PPY : *Pongo pygmaeus*; GGO : *Gorilla gorilla*; PPA : *Pan paniscus*; PTR : *Pan troglodytes.*

— *Hominidae*:

HSA : *Homo sapiens.*

12 se retrouvent d'ailleurs chez plusieurs Cercopithécoïdes, traduisant leur origine très ancienne.

Ainsi, de proche en proche, peut-on reconstituer l'aspect des chromosomes, chez des formes ancestrales ayant disparu depuis des dizaines de millions d'années.

La cytogénétique reste incapable d'apporter des éléments de datation, et il serait très présomptueux d'affirmer que la survenue des remaniements chromosomiques ait une certaine régularité.

Le seul moyen valable de datation demeure la paléontologie, encore qu'il faille en connaître la valeur souvent approximative.

Néanmoins, en se basant sur les datations des plus anciens cercopithécoïdes, platyrhiniens ou prosimiens reconnus, on peut considérer que:

— la séparation prosimiens-simiens remonte à probablement plus de 50 millions d'années (point B, figure 4);

— la séparation platyrhiniens-catarhiniens remonte à probablement plus de 40 millions d'années (point 5, figure 4);

— la séparation Cercopithécoïdes-Pongidae + Hominidae à probablement plus de 30 millions d'années (point D, figure 4).

Ainsi, les carrefours des figures 4 et 5 peuvent être datés, et de même les différents remaniements chromosomiques.

Ceci aboutit finalement à dater les différents chromosomes d'une espèce. Ainsi, les chromosomes humains 1, 2, 4, 9, 18 et Y, qui n'existent que dans notre espèce sous cette forme, ont subi leur dernière mutation récemment, depuis que les hominidae se sont détachés des Pongidae. Ces chromosomes ont au plus une dizaine de millions d'années environ.

Les chromosomes humains 14 et 15 se sont formés après la séparation d'avec les cercopithécoïdes, soit il y a entre 20 et 30 millions d'années etc...

Les plus anciens chromosomes semblent être les 13 et 20 qui étaient sans doute déjà très semblables à ce qu'ils sont aujourd'hui chez l'homme, chez des mammifères non primates, il y a une centaine de millions d'années.

Il est donc finalement possible d'apprécier l'âge « moyen » du caryotype d'une espèce, et de différencier les espèces selon qu'elles possèdent un caryotype très évolué ou très primitif.

Le primate dont le caryotype est resté le plus ancestral est sans doute le microcèbe *Microcebus murinus*, prosimien de Madagascar.

Parmi les simiens les singes capucins *Cebus capucinus* ont aussi gardé un caryotype primitif.

Parmi les catarhiniens, les macaques et babouins (*Cercopithécidae*) et l'orang-outang (*Pongidae*) ont aussi gardé de nombreux chromosomes ancestraux.

Le caryotype humain a un niveau d'évolution, comparable à celui du chimpanzé et du gorille, et à celui de beaucoup de Cercopithèques.

La position évolutive de l'homme

Cette question, qui trouve, pensons-nous, sa réponse ici, a été souvent soulevée et fait l'objet de grandes controverses.

Pour situer le niveau de ces controverses, beaucoup de paléontologistes estiment que les Hominidae se sont détachés très tôt, dans l'histoire des primates où ils ont formé un rameau parallèle à celui menant aux Pongidae, sans qu'il y ait eu d'interconnexions. Une telle interprétation amènerait à penser que les Hominidae sont d'origine très ancienne, remontant à plusieurs dizaines de millions d'années.

Cette opinion est en total désaccord avec les résultats biologiques en général, et cytogénétiques en particulier.

En effet, l'étude précise des remaniements chromosomiques nous apprend que les Pongidae et l'homme ont tous acquis, en commun 6 remaniements (figure 5). Le rameau menant à l'orang-outang (Pongidae) s'est ensuite détaché, avant que 5 remaniements ne soient acquis en commun par le gorille et les 2 espèces de chimpanzés, qui sont aussi des Pongidae, et par l'homme.

Ceci ne peut recevoir qu'une seule interprétation raisonnable: il y a eu une étape Pongidae assez longue, avant que les rameaux menant au gorille, aux chimpanzés et à l'homme ne se séparent.

Le moment de cette séparation mérite d'ailleurs quelques commentaires, car 2 remaniements sont acquis en commun par les ancêtres de l'homme et des chimpanzés, tandis que 3 autres remaniements sont acquis en commun par les ancêtres des chimpanzés et du gorille.

Ce partage de remaniements montre qu'il n'y a pas eu de séparation stricte après l'acquisition de chaque mutation chromosomique, mais qu'il y a eu au contraire une évolution de type populationnel, au cours de laquelle les chromosomes remaniés se sont distribués diversement.

Bien qu'il soit, comme nous l'avons dit, imprudent de considérer la survenue des mutations chromosomiques comme une horloge biologique, on peut toutefois sans grand risque d'erreur, avancer que cette période d'évolution populationnelle a été assez longue, durant peut-être plusieurs millions d'années.

Enfin, apparaît le rameau propre aux Hominidae, avec l'acquisition de 4 à 5 remaniements seulement.

Ce rameau, en terme de mutations chromosomiques est tout à fait comparable à celui menant aux gorilles ou aux chimpanzés, ce qui renforce l'idée d'une trifurcation de ces 3 rameaux.

On peut donc conclure que l'hominisation a été un phénomène rapide à l'échelle de l'évolution, qui n'a pas excédé en durée les phénomènes de spéciation de chacun des autres primates.

Ces données cytogénétiques sont actuellement peut-être les plus complètes et les plus précises en ce qui concerne la phylogénie des primates, mais en tous cas, elles ne sont jamais en contradiction avec les autres études biologiques réalisées jusqu'ici telles que l'analyse de protéines, l'enzymologie, l'hématologie et l'immunologie.

Souhaitons donc que ces évidences soient un jour entendues de tous les paléontologistes.

Les comparaisons chromosomiques avec les mammifères non primates

Nous venons de voir que la cytogénétique permet non seulement de comparer des espèces proches, mais aussi des espèces fort éloignées à l'intérieur de l'ordre des primates.

Ces dernières années, les améliorations techniques nous ont amenés à pousser plus loin les comparaisons, c'est-à-dire à comparer des espèces appartenant à des ordres différents. Très rapidement, il est apparu que dans les autres ordres de mammifères aussi, il existe (fort heureusement pour le cytogénéticien) des espèces ayant conservé un caryotype très ancestral.

Certains ordres, comme les lagomorphes semblent n'avoir subi qu'une évolution chromosomique minime, de sorte que le lapin, et plus encore le lièvre, pourraient ne différer que par moins de 10 remaniements des ancêtres de l'ordre.

Des conclusions similaires sont obtenues à propos des carnivores, et les études en cours sur d'autres ordres vont également dans ce sens.

Il est ainsi très intéressant de constater que la reconstitution du caryotype ancestral des primates, des lagomorphes et des carnivores, réalisée indépendamment, aboutit à des caryotypes très semblables, avec de nombreux chromosomes identiques.

Ceci permet de penser que les ancêtres communs à ces différents ordres possédaient eux-mêmes ces chromosomes, et c'est donc à la reconstitution de ce caryotype mammalien ancestral que nous tendons maintenant.

Ce retour aux sources permet donc de comparer directement les rameaux terminaux des différents ordres. Ainsi, les caryotypes de l'homme et du lapin diffèrent par moins d'une cinquantaine de remaniements et de nombreux segments chromosomiques communs sont faciles à retrouver [2]. Les caryotypes de l'homme et du chat, pour rester dans des espèces bien connues diffèrent à peine plus.

Ceci nous enseigne qu'il n'y a pas eu de grands bouleversements chromosomiques au moment où les ordres de mammifères se sont différenciés.

Ces résultats, encore trop nouveaux pour être détaillés ici ouvrent aussi la voie à une étude comparée, aussi bien pour la physiologie que la pathologie, de grande ampleur.

On peut également espérer pouvoir établir bientôt avec précision la phylogénie des ordres de mammifères entre eux.

BIBLIOGRAPHIE

[1] DUTRILLAUX B., *Chromosomal evolution in primates: tentative phylogeny from* Microcebus murinus (Prosimian) *to man.* « Hum. Genet. », *48*, 251-314 (1979).

[2] DUTRILLAUX B., VIEGAS-PEQUIGNOT E. et COUTURIER J., *Très grande analogie de marquage chromosomique entre le lapin* (Oryctolagus cuniculus) *et les primates, dont l'homme.* « Ann. Génét. », *23*, (1), 22-25 (1980).

THE ORIGIN OF MAN IN THE CONTEXT OF THE CHANGING BIOLOGICAL PARADIGMS

G. SERMONTI
Istituto di Biologia Cellulare, Università di Perugia

The myth of the origin of Man

The emphasis given by the philosophy of the nineteenth century to history led to the replacement of the problems regarding the "nature" of the organisms with those on their "origin". The dominant interest in Ontogenesis was substituted by the rising concern regarding Phylogenesis, to such an extent that Ontogenesis was viewed as a result — not only as a recapitulation — of Phylogenesis (E. Haeckel). In this context the problem of Man (whose homologies with the apes had already been recognized by Linneus a century earlier) became the problem of his ancestry. The Darwinian theory of Evolution did not provide a solution to the problem, or a method of investigation, but rather converted it into a truism (there must be an origin for everything), to be possibly illustrated by examples, but not amenable to confutation. Man had to be derived from a more primitive primate (symbolically an ape) through a process of gradual adaptation, during which it gained the traits that made him the dominant mammal. Only the details of the process had to be specified: through which steps was the human condition achieved? Why was such and such trait selectively advantageous so as to justify its prevalence? When and where did the process take place? Before a solution was found to any minor aspect of the problem a large space was available to the imagination, and the origin of Man became a favorite topic for intellectual exercise.

Durant (1981) depicted in these words the situation: "Could it be that, like primitive myths, theories of human evolution reinforce the value-systems of their creators by reflecting historically their image of themselves and the society in which they live? Time and again, ideas on human origin turn out on closer examination to tell us as much about the present as about the past, as much about our own experiences as about those of our earliest ancestors".

Notwithstanding a noticeable crop of information collected in the last decades, the drama of human origin never avoided a mythological flavour, due to the dominant "ideologies" of the investigators. This was clearly stated by D. Pilbeam (1978). "I have come to believe that many of the statements we make about the hows and whys of human evolution say as much about us, the paleontologists and the larger society in which we live, as about anything that 'really' happened".

Since the publication of the *Descent of Man* by Charles Darwin, the theory on the Origin of the Species was reshaped so many times that one may wonder if it is still legitimate to adopt the old paradigms (adaptation, descent, progress, improvement, etc.) in order to solve the problem of human origin, and even if the problem is still there, in its primitive form. The more we know on human phylogeny, the less is the light it throws on the understanding of human nature, of human peculiarities, of human destiny.

Inactuality of the descent problem in the new biology

What is the picture of the history of life we face today? What is the theory on speciation we have eventually elaborated? What is the prevailing attitude in front of the problem of the emergence of a form?

The answers are complex and all but generally agreed. I will only anticipate a few essential points just to show how much our views have departed from the original Darwinian position. First, the gradual character of the transformation of morphological species was more and more challenged; it has been suggested by Eldredge and Gould (1972) that species appear abruptly and then remain stable for millions of years. Second, genetic species are not formed through adaptive changes, but mainly through geographical isolation followed by neutral changes (see Lewontin, 1974).

Third, the theories on the development of the forms are now considered of primary importance and preliminary to any answer about the modification of the forms (Goodwin and Webster, 1981).

In short, *stasis and saltation* in the paleontological record, *neutralism* in population genetics and *physical constraints* in biological pattern formation are among the key features in modern biology. They oppose to graduation, selection and historicism of the neo-Darwinian picture. Are the problems of descent still of major relevance in the context determined by these new paradigms? If a species differs sharply from its ascendant, not as a response to environmental pressures but as a result of the emergence of a new developmental pathway, the identification of the ascendant and the study of its habitat become but marginal information in the understanding of the biology of the new form.

Taxa divergence and macromolecular comparison

Amino-acid sequence comparison among homologous proteins in related species and nucleotide sequence comparison among homologous DNA fragments, together with DNA hybridization data and immunological measurements have lent themselves to the reconstruction of phylogenetic trees.

These techniques have been amply discussed in relation to primate evolution by R. F. Doolittle and D. Perlman in the course of this Symposium, and I will therefore confine myself only to some comment and consideration.

The molecular observations are essentially consistent, and, if accepted as a criterion for measurement of line divergence, they lead to a general picture, on our side in agreement with the neo-Darwinian expectation, on the other in serious disagreement with that and to some extent irrelevant to the testing of the theory.

a) The extant species derive from one (or a few) primitive ancestors through branching lines. This conclusion is in good agreement with the Darwinian prophecy.

b) All the amino-acid (or nucleotide) substitutions are however, with no exception, *neutral*. This means that natural selection does not operate at the level of protein structure. This is in complete disagreement with the neo-Darwinian expectation. The amino-acid or nucleotide substitutions are, in a sense, comparable with the isotope decay in rocks. They are a reliable record of the time elapsed since the formation of the sediment, but are by no means *the cause* of its age. Similarly the number of differences in amino-acid residues between homologous proteins in two species, as well as data on DNA sequences or hybridization, are a measure for dating their divergence, but by no means *the cause* of such divergence.

c) The pattern of divergence as testified by the macromolecular comparisons does not say anything about *the mechanism* of the divergence, save the fact that the macromolecular alterations themselves are not involved in the mechanism. They would not otherwise be such a reliable timing clock. The divergences might be due to geographical or developmental diversifications, to chromosomal or genic isolations, to gradual or abrupt changes, to internal or external pressures and be accompanied or followed by large or negligible morphological differentiations. At the extremes, two homologous genes may diverge at the splitting of two Phyla or Classes, or diverge within the same species, after the duplication of a common ancestor gene.

The origin of "genetic" species, i.e. the establishment of reproductive barriers between two (or more) populations, certainly results in the divergence between phyletic lines testified by the molecular comparison. The origin of larger taxa is however in a less clear connection with the splitting of reproductive lines.

If we assume, as Darwin did, that taxonomic differentiation gradually proceeds to generate higher ranks, from species to genera to family to orders etc., the *nodes* of divergence would be at the species level and would therefore possibly antedate by millions of years the emergence of major taxonomic groups. If the latter appear abruptly, and are secondarily subdivided into groups of lower rank, their origin would coincide with the nodes of molecular divergence. Molecular comparison by itself cannot decide between the two alternatives, because it does not deal with morphological differentiation, but the two patterns of emergence — from general to particular or viceversa — can well be tested on paleontological ground. The available evidence suggests — contrarily to the Darwinian expectation — the early appearance of the major taxa (Grassé, 1973). This makes comparison between paleontological and molecular record meaningful, but again on a non-Darwinian assumption.

Morph emergence

There has recently been a revival in the interest in ontogenesis in relation to evolution. A Dahlem Konferenz on *Evolution and Develop-*

ment (1982) has emphasized the new approach. "The idea that evolution and development should be brought together is not new, wrote J.T. Bonner, nor has it been totally neglected in recent years. What is new is that there is suddenly a general consensus that this is precisely what is needed at this time". The idea is that evolution, or any kind of transformation, is a shift in the ontogenetic development, and that we need therefore to have a better insight into ontogeny if we want to understand evolution. The emphasis on developmental, or internal, constraints in evolution is clearly expressed by the statement that only a limited number of forms are *biologically possible.*

Using a metaphor introduced by C. H. Waddington (1957), the development of an organism can be represented as the flow of a river along a system of valleys forming the so-called "epigenetic landscape". A series of successive "decisions" are taken at the *bifurcation points,* which eventually define the configuration of the organism. In admittedly oversimplified terms, a new form may historically emerge from another, just by a change in option at one bifurcation point. A new predetermined possibility is thus brought into existence. Pedomorphosis is a good example of this evolutionary process.

An adult regresses to a larval (or foetal) stage, abandoning a basin, backwards up to a bifurcation node. Later "the river" flows down again along a different basis, drawing a new adult configuration. The two adults have common precocious stages of development, and diverge in later stages. This model would agree with the Von Baerian view of comparative embryology, would not involve "intermediate" forms, would not establish any historical priority or irreversibility, and would provide a criterium for an ontogenetically grounded taxonomy.

Let us consider a number of constraints amenable to justify the clustering of organisms in the so-called "morphospace". We may assume *phylogenetic* constraints: organisms are grouped just because of their common ancestry. We may emphasize *adaptive* constraints, producing clustering around some "adaptive peaks", as S. Wright suggested in the stream of the Darwinian tradition. *Mutational* constraints have also been considered, i.e., limitations imposed by the structure of DNA. *Developmental* constraints appear, among the others, the most constant, essential, and constructive ones. Generative rules operating in the developmental process limit the morphological types which may appear during the life history. This idea can be traced back to D'Arcy W. Thompson. In his *Growth and Form* (1942), life is seen as the result of geometric rules, of physical laws which severely limit the possible forms and give to living beings their elegance, harmony, meaning. The problems of form are first of all mathematical problems; the problems of growth are essentially physical problems. The time dimension does not affect them. As P.F.A. Manderson (1982) wrote, "the evolutionary process (is hecoming) intelligible in terms of *laws* intrinsic to developmental processes as well as *contingencies* arising from extrinsic or environmental influences".

The process of development was described by L. Wolpert (1972) as a two-step process. "First the cells are *assigned positions* in a coordinate system, and the cells then *interpret* their positional values hy appropriate cell differentiation. The interpretation will depend on the genetic constitution of the cell and its developmental history".

Mutational changes and the "logic" of development

Morphogenetic changes in evolution may be due to alterations either in position assignement (major changes) or in position interpretation (minor changes). The latter allow the description of most of the transformations which we see in the course of evolution. We know little of the role played by structural gene mutations in position interpretation changes. It is quite possible that they only have a stabilizing effect. As a matter of fact we find genes functionally identical in species so unrelated as a man, a whale, a butterfly, a spinach, or even a mold. The genes are responsible for the chemical constitution of the organisms, and what makes the organisms different is not their peculiar biochemistry, but the distribution in space of essentially the same constituents. As F. Jacob wrote: "What distinguishes a butterfly from a lion, a hen from a fly or a worm from a whale is much less a difference in chemical constituents than in the organization and distribution of these constituents... It is not hiochemical novelties which have generated diversification of organisms. In all likelihood, it worked the other way around". Biochemical novelties are the *result* of genetic divergence. The genetic constitution might well be an essentially universal endowment of all organisms. I make this statement in spite of the known fact that single gene differences are known which produce large effects in morphology. They produce, however, only teratological effects, with reduction, misplacement or amplification of parts. Their great interest in the experimental approach to morphogenesis does not imply that they are the types of events which have shaped organisms, as biochemical (auxotrophic) mutations have certainly not been responsible for the building up of cellular biochemistry.

Some large morphological mutations, particularly in Drosophila, deserve to be mentioned, for they mimic the emergence of new forms, although their actual role in evolution is probably irrelevant. They are technically important in the investigation of the ontogenetic processes, particularly in illustrating the role of the maternal effects (position assignment) and the phenomenon of interpretation of positional values. Let us consider some maternal effect mutations, as *bicaudal* or *dorsal* mutations in Drosophila. The first causes the production of embryos with two posterior ends, the second with two dorsal sites.

Other mutations affect segmentation, producing deletion or fusion of segments. The so-called homeothic (or systemic) mutations may transform antennae to legs or palps or replace thoracic posterior compartment structures with anterior ones, so as to produce adult flies with four wings (the well-known bithorax). It has been suggested that these systemic mutations or *macromutations* may represent the mechanism of major changes in evolution. R. Goldschmith used the term of "hopeful monsters" to indicate possible great novelties in evolution. I am, in general, suspicious of any transfer from the lab experience to nature. The most plausible role of loci like those of the *Antennapedia* or *Bithorax* complexes (the so-called homeothic loci) is in the *stabilization of positional information*. As T. C. Kaufman and B. T. Wakimoto assert, "Positional information specified during ogenesis and refined during embryogenesis activates or inactivates these loci in a sequentially patterned fashion. Once active, the product of the homeothic genes selects or represses batteries of other genes".

Interpretation requires a language, a code, and a set of rules to achieve some spacial configuration, *geometrical rules* as D'Arcy W. Thompson called them. The embryologists are on the tracks of such rules, of understanding a code at a higher level than the genetic code: a spacial, tridimensional set of rules which eventually will define which forms are developmentally possible, will establish the physical internal constraints of living matter. In the foundation of the new paradigms of developmental biology, genetics, although useful as a tool of study, may be largely irrelevant. As pointed out by G. Stent (1981), the genetic composition of different taxa is probably much more constant than their diversity would suggest, and different genetic endowments could provide the substrate for the same morphogenetic rules. Also molecular specificity might be irrelevent, as first suggested by Wolpert (1978) after his observations of the diverse chemical signals used by slim molds for aggregation. As A. Sibatani (1981) states: "apparently it is not molecular evolution, but evolution of what we conceive as 'logical' structure in a developing system that would be important in some new paradigm".

Molecular differentiation is so significant in tracing phylogenies, just because it is not relevant in determining their course.

On the phyletic gradualism

The Darwinian philosophy involves gradual changes at the origin of the taxa. It opposes catastrophism and, in a sense, the Darwinian world is one in which everything is created while nothing happens.

A gradual change in the traits of a species is easily understandable: it may be neutral or adaptive, genetic or environmental, or perhaps epigenetic. A gradual change in the genetic structure of a species is also perfectly in line with Mendelian population genetics. The critical point is whether such gradual change is a variation within a morph or a transition wherefrom a new morph emerges at a given point. Can *gradual alteration* produce the *new*, or is its potentiality limited to some quantitative variation of no relevance for the problem of emergence of new forms? It is well known that western man is rising in height about one mm per year, or that the frequency of diabetics is steadily increasing in the developed countries. These changes will not, however, eventually produce a new species. The demonstration that a given trait, like cranial capacity, changes smoothly in the paleonthological record of hominids (Cronin *et al.*, 1981) does not prove the gradual emergence of a new form, simply because it does not prove that a new form has emerged! Great variations in cranial capacity can be recorded in present human specimens with absolutely no relevance to their human nature.

Indeed gradualism is by definition a modification with no real change. Thus, either graduation is connected with some significant abrupt change in shape (and the latter is the true evolutionary event) or it doesn't say anything, either on the question of speciation or on that of form emergence. Graduation is but a particular kind of *stasis*. Gradual transformation may, however, occur in the relative size of different parts of a form, in their proportion. Up to a certain degree it may not exceed the natural disproportions within a morphological species. Two problems have thus to be faced: when is a *deformation* such that we can consider one form as related to another and yet a different form? Is there any available evidence that two forms are connected by a graduated series of intermediate forms? A chimpanzee, a gorilla, an orang-utan and a human are different forms, but evidence is lacking of anything intermediate among them. The same holds for *Homo* and the various australopythecinae. What can we assess about the various specimens attributed to the genus *Homo* and given different specific names as *habilis, erectus* and *sapiens*? Y. Coppens (1980) is hesitant in granting them the rank of different species: "Tout a l'air de se passer comme si on avait désormais affaire à un continuum, plus ou moins panmictique, chargé de rapports multiples et complexes dans le temps et dans l'espace". Thus continuity, i.e. graduality, is indicative of membership in a single entity, a single essential form. The two concepts of gradualism and species transformation are to some extent conflicting, and an unprejudiced epistemological analysis of the subject is badly needed before we can speak of a gradual replacement of a species by another in the course of time (anagenesis).

Conclusion

It is a common opinion that "The structure of animals, their anatomy, tells us much about their relationship one to another. The structure of their body protein tells us even more" (see Cherfas, 1982). In fact the two informations do not speak of the same thing. Molecular comparison tells us about the time elapsed since the splitting of lines leading to extant animals; anatomical comparison illustrates the end result of processes which occurred since the splitting. Molecular divergence is but an impassive clock, anatomical divergence testifies the dramatic events of life. An evolutionary tree of primates derived from molecular comparison and deprived of the living species at the top of the branches would not help at all in depicting the present forms. The present forms may be deceptive in reconstructing their tree. While morphological classification would predict that chimpanzee and gorilla should be more like orang than man, molecular comparison reveals a close affinity among chimp, gorilla and man, and an early splitting of the orang branch.

Comparative embryology is perhaps the most revealing analysis in tracing the emergence of different forms. The differences among them are in the peculiar interpretation of the positional values assigned to their various tissues during foetal development. In this respect man appears to be the most juvenile form among primates, showing as adult the closest resemblance to the primate foetus. The problem of his form determination may be posed as a problem of ontogenetic divergence rather than of phylogenetic splitting. In this respect no extant primate is more primitive or "evolved" in respect to the other, and even extinct forms had their complete developmental cycle and by no means appear to be more childlike or less complete than the later animals.

No form (man included) is — in the ontogenetic context — a *derived* form or an *improved* form in respect to some "primitive" ancestor. Man does not derive from Primates (as Birds do not derive from Reptiles), but in the deceitful sense by which any form may be considered a derivative "from" the larger group to which it belongs.

Neither molecular comparison, nor comparative anatomy and possibly not even comparative embryology can help in providing us with the ultimate answer: did the extant primate forms emerge abruptly from clearly different forms, or were they shaped gradually? Paleontology holds the key to the problem, although it is not much inclined to reveal it. Sudden emergence seems to be the answer, but we are not prepared to accept it. We have names for pre-human forms. We call them ape-men, sub-humans or brutes. Did they ever exist, or do they rather belong to an obsolete mythology?

REFERENCES

BONNER J. T. (Ed.), *Evolution and Development.* Dahlem Konferenzen. Springer-Verlag, Berlin, pp. 1-16 (1982).

CHERFAS J., *Proving the pattern of life.* « New Scientists », *94,* 484-487 (1982).

COPPENS Y., *L'origine du genre Homo.* In « Colloques internationaux du C.N.R.S., N. 599: Les processus de l'hominisation », (1980).

DURANT J. R., *The myth of human evolution.* In « Riv. Biol. », *74,* 125-151 (1981).

ELDREDGE N. and GOULD S. J., *Punctuated equilibria: an alternative to phyletic gradualism.* In « Models in Paleobiology », T.J.M. Schopf, ed. Freeman, Cooper & Co., San Francisco, pp. 82-115 (1972).

GOODWIN B. C. and WEBSTER G. C., *Rethinking the origin of species by natural selection.* « Riv. Biol. », *74,* 11-26 (1981).

GRASSÉ P.P., *L'évolution du vivant.* Albin Michel, Paris (1973).

JACOB F., *Evolution and thinking.* « Science », *196,* 1161-1166 (1977).

KAUFMAN T. C. and WAKIMOTO B. T., *Genes that control high level development switches.* In « Evolution and Development », J.T. Bonner, ed. Dahlem Konferenzen. Springer-Verlag, Berlin, pp. 189-205 (1982).

LEWONTIN R. C., *The genetic basis of evolutionary change.* Columbia University Press, New York and London (1974).

MANDERSON P. F. A., *The role of development in macroevolutionary change. Group report.* In « Evolution and Development », J. T. Bonner, ed. Dahlem Konferenzen. Springer-Verlag, Berlin, pp. 273-312 (1982).

PILBEAM D., *Rethinking human origins.* « Discovery », *13,* 2-9 (quoted in DURANT J. R., 1981), (1978).

SIBATANI A., *Two faces of molecular biology: revolution and normal science.* « Riv. Biol. », *74,* 279-296 (1981).

STENT G.S., *Strength and weakness of the genetic approach to the development of the nervous system.* « Ann. Rev. Neurosci. », *4,* 163-194 (1981).

THOMPSON, D'ARCY W., *On Growth and Form.* 2nd ed. Cambridge University Press, Cambridge, MA (1942).

WADDINGTON C. H., *The strategy of the genes.* Allen and Unwin, London (1957).

WOLPERT L., *The concept of positional information and pattern formation.* In « Towards a Theoretical Biology », vol. 4. *Essays,* Waddington C.H. ed., Edinburgh University Press, Edinburgh, pp. 83-94 (1972).

WOLPERT L., *Pattern formation in biological development.* « Sci. Am. », October (1978).

SUMMARY

A working group of twelve scholars from six countries convened on May 24-27, 1982, at the Pontifical Academy of Sciences at the Vatican, to discuss recent advances in our knowledge of *primate evolution*, with particular reference to reconciling the paleontological evidence with evidence from molecular biology.

The process of the evolution of living beings is the accepted basis of modern biology. More specifically, in the field of primate studies, common ancestry is a highly confirmed and widely supported hypothesis.

The working group reviewed the fossil, morphological and biochemical evidence for temporal and genetic relations among fossil and living primates and assessed the state of the early hominid fossil record. A major issue during the past two decades has been this question: whether the various living apes and man descended from a common ancestor as long as 20 million years ago (the Early Divergence Hypothesis) or whether the ape-hominid split occurred as recently as 5-7 million years ago (the Late Divergence Hypothesis). The principal evidence for Early Divergence is the fossil record of the hominoid *Ramapithecus*, dated from 7-16 million years, and considered by some to be hominid (on the human line). The strongest evidence for Late Divergence is a mass of biochemical data showing about 99% 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 million years ago. If *Ramapithecus* were ancestral to the apes or to apes and humans, rather than a hominid, the fossil and biochemical evidence could be reconciled. Therefore, the working group paid particular attention to current evidence for the phyletic status of *Ramapithecus*. They also reviewed the growing hominid fossil record in Africa which delineates more clearly the course of hominid evolution during the past 4 million years, and they paid special attention to the early appearance of bipedal locomotion and the later expansion of the brain.

E.L. SIMONS (USA) began the discussion with a review of anthropoid (higher primate) fossils. The earliest record of monkeylike and apelike primates comes from the Fayum, Egypt, with an estimated age of 25-35 million years. According to Simons, several groups have been identified: two genera, *Apidium* and *Parapithecus*, which have monkeylike teeth, and two genera, *Propliopithecus* and *Aegyptopithecus*, which have apelike teeth. A newly discovered genus, to be designated *Qatrania*, resembles *Parapithecus* but is much smaller; and older. Another of the older genera, *Oligopithecus*, has both monkeylike and apelike dental features, perhaps slightly more of the latter. *Aegyptopithecus* bears dental resemblances to apes but has limb bones resembling those of New World howler monkeys. Therefore, *Aegyptopithecus* may be ancestral either to the Old World monkeys *and* the hominids (which includes both ape and human lineages), or to the hominoids only. Here, as in so much of primate evolution, the dating of divergences between lineages becomes critical. The molecular data have been interpreted to suggest a split between Old and New World monkeys at 35-40 million years and between Old World monkeys and apes at 20-22 million years ago, which would place *Aegyptopithecus* between these two points of branching; whereas paleontologists have tended to date these branchings much earlier. Simons noted that the ecological and dental evidence indicates that these early anthropoids lived in forests, high in the trees, and ate leaves and fruit, which represented a departure from their presumed insectivorous ancestors. There were probably considerable size differences between males and females. The earliest primate fossils with teeth like those of living Old World monkeys have been found in North and East Africa dated 16 to 20 million years.

Turning more specifically to hominoid evolution, L. GREENFIELD (USA) reviewed the conflicting interpretations of ape and human ancestry, focussing on the disputed status of *Ramapithecus*. The previously widely held belief that *Ramapithecus* was hominid implied an early divergence (minimum 15 million years) between apes and hominids. This has been a major reason why many anthropologists would not accept the growing molecular evidence for a much later divergence (5-7 million years). Thickly enamelled molars have been proposed as evidence of a phylogenetic relationship between *Ramapithecus* and *Australopithecus*. In Greenfield's opinion, this trait is of limited phylogenetic significance and does not support the inferred direct relationship. He considers that such molecular biological data as DNA and protein similarities more accurately reflect the genetic relationships of living primates and provide a useful starting point for the interpretation of the fossil record. These data effectively eliminate the possibility that *Ramapithecus* was hominid.

D. Pilbeam (USA) stressed that the preferred phylogeny of fossil and living primates should be one which fits best all the available data — molecular, morphological and paleontological. His reevaluation of hominoid evolution and hominid origins, including the status of *Ramapithecus*, began in the early 1970's, stimulated by growing molecular evidence and new fossil finds. Molecular data provide the most reliable evidence for the sequence of branching. The fossil record, together with the comparative anatomy, of recent forms, enables scholars to formulate hypotheses as to which morphological features are primitive and which derived. Among early Miocene forms, *Proconsul africanus* is accepted as hominoid; it is apelike but not specifically like any living ape. Miocene hominoid fossils in Africa (dated to 14-18 million years ago) and Eurasia (7-16 million years ago) are generally found in conditions indicating forest and woodland habitats. Limb bones attributed to *Ramapithecus* and *Sivapithecus* indicate an arboreal adaptation rather than a ground-living way of life such as is characteristic of hominids.

Sibley's DNA hybridization data have been calibrated by Pilbeam on the basis of 16 million years for the separation of the orangutan and African ape lineages. On this basis the following divergence times are obtained: chimpanzee-human 7 million years; gorilla-human 10; gibbon-human 18; cercopithecoid-ape 22.5. (Some molecular anthropologists would place the orangutan divergence at 10-12 million years, which would make the other branch points proportionately later). Pilbeam stressed that there are almost no hominoid fossils known in Africa between 4 and 14 million years. This is a very critical period in which the last common ancestor of man and the African apes probably lived. There is also no fossil record at all for the gorilla and chimpanzee lineages. Pilbeam suggests that *Ramapithecus* and *Sivapithecus* were related to the orangutan lineage. The record for undoubted hominids begins in Africa about 4 million years ago.

Y. Coppens (France) reviewed the African hominid fossil record which begins with a possible hominid molar at Lukeino at 6.5 million years and a lower jaw fragment at Lothagam at 5-6 million years, but with undoubted hominid evidence in East Africa by 4 million years ago. This evidence comes mostly from sites at Hadar (Ethiopia) and Laetoli (Tanzania) but also from Kanapoi, Chemeron, Omo and so on. In 1978 Coppens and others designated this material as a new species, *Australo-*

pithecus afarensis. Variability in dental and postcranial features was attributed at that time to a great degree of sexual dimorphism. In closer study of the evidence, especially the limb bones, Coppens has concluded that there were possibly two species at Hadar rather than one, in this early time level between 4 and 3 million years — one being more archaic than the previously described australopithecines, and one being more similar to *Homo.* Coppens emphasized that anatomically true hominids undoubtedly existed by 4 million years ago. He proposed a phylogenetic model which pushes the branching of australopithecines to a possibly pre-australopithecine stage at about 6 or 7 million years ago.

One hallmark of the human family (Hominidae) is the acquisition of upright posture and a bipedal mode of locomotion. E. Boné (Belgium), reviewed the skeletal evidence for Miocene through Middle Pleistocene hominids and discussed the structural basis for bipedalism and indicated its presence in the fossil record by at least 3 million years ago. Boné discussed the possible existence of two locomotor patterns among the australopithecines. He addressed himself to the question: under what sort of ecological circumstances did bipedalism arise and develop? At present there seems to be no simple, direct correlation between morphology, taxonomy, and ecology. Although ecological conditions must have played a role in the origin of bipedalism, their precise influence is not clear. There might have been different ecological settings in East and South Africa for the early time period prior to 2-2.5 million years ago.

The paleo-ecology of East and South Africa received much discussion and Y. Coppens pointed out that at a recent conference on Plio-Pleistocene climates, the evidence was interpreted as indicating a shift from wetter to drier conditions in East and South Africa about 2.3 million years ago.

V.V. Tobias (South Africa) reviewed a number of changing concepts in hominid evolution. Among these were the existence of early hominids which were ancestral and those which were not ancestral, to later and modern man; the extinction of some early hominids; the questions of continuous or discontinuous change, of gradualism or punctuated equilibria, of supposedly Darwinian or non-Darwinian patterns of change; the relationship between speciation (the origin of new species) and cladogenesis (the branching of a lineage), and the probable occurrence of reticulate (network) evolution in Quaternary man. He showed how dramatically the numbers of fossil sites and of hominid fossils had increased in recent decades and indicated that of the order of 485 individuals were now represented by the available early hominid fossils from African deposits between 4.0 and 1.0 million years old. Tobias examined these hominid fossils and addressed especially brain evolution and its relation to the origin of speech capabilities. He emphasized, as did Boné, that the development of bipedal locomotion involved structural modifications throughout the body, from the cranial base to the feet. New fossils from recent Sterkfontein excavations were shown. Reviewing the evidence of endocranial casts, Tobias stressed the trend toward a remarkable increase in absolute and also in relative brain size during the Plio-Pleistocene. With the limited size of the birth canal, the size of the brain at birth has become a progressively smaller percentage of adult brain size; more and more brain growth occurs during postnatal life. Tobias argued for the presence of speech (albeit rudimentary) in *Homo habilis* on the hasis of endocast features indicating the presence of Broca's and Wernicke's areas and of a probably partially hominized vocal tract. He proposed that the stone tool technology of these early hominids and other archeological evidence reflected emerging cultural patterns and learned technical skills that necessitated speech for their transmission. Coppens pointed out that there is evidence from Omo and Hadar of stone tools at about 2.5 million years ago, while a few suggestive traces may be as old as 3 million years.

In reviewing techniques based upon molecular biology, R. DOOLITTLE (USA) explained that molecular data are of several kinds, each providing information of different precision, on species specificity and molecular clocks. For example, immunological techniques can show the degree of difference between species but cannot pinpoint how many changes have occurred at the base pair level. DNA hybridization compares selected subsets of the DNA's of two or more species. Of the approximate 10^9 base pairs in a genome, only about 1% is expressed as proteins. Both amino acid sequencing of proteins and the sequencing of DNA bases provide quantification of evolutionary changes. Doolittle asserted that the concept of neutral mutation is strongly supported by all of these data and is particularly well illustrated by "pseudogenes" which change rapidly without any apparent selective pressures against the base pair substitutions. Doolittle concluded that pseudogenes, particularly the alpha-1 hemoglobin pseudogene, represent a class of DNA segments that offer an unusual opportunity for assessing the relationships of extant higher primates.

J.M. LOWENSTEIN (USA) presented some results of a new radioimmunoassay technique that explores the immunological relationships between proteins of fossil and living species. He has applied this method successfully in the study of the evolutionary affinities of extinct elephants, sirenians, marsupials, and primates. *Ramapithecus* and *Sivapithecus* bone fragments showed more or less equal affinity with orangutan, gorilla and gibbon serum proteins, somewhat less affinity with those of man and chimpanzee and much less with those of monkeys and non-primates. These preliminary results suggest that though the *Ramapithecus/Sivapithecus* group were hominoid, they were not hominid. Lowenstein also reported for the first time that collagen reactions on the Piltdown jaw and canine tooth identify each as being orangutan.

J. LEJEUNE (France) raised the important question of the relationship between the origin of a species and its chromosomal structure. A proposed aphorism: one species — one karyotype, summarized the available cytogenetic data. In reviewing the homologies between *Homo* and the great apes as described by Dutrillaux, Lejeune pointed out that in all some 14 chromosomal rearrangements separate man, orangutan, chimpanzee and gorilla from one another. The peculiar case of Chromosome 2 makes chimpanzee appear closest to man. With advances in technology, it is now possible to study the banding patterns of the chromosomes and more specifically, delineate the species-specificity and possible changes among closely related groups. Lejeune argued that the differences between man and chimpanzee are not so much in the words (the genetic code) but in their style, in the way the words are put together. It is not the accumulation of small mutations that produces new species, but rare major chromosomal rearrangements which at once modify genetic expression and produce reproductive isolation. As a result, a new species emerges quite suddenly in a very restricted, highly consanguineous group. On this basis he pointed out the fact that the hypothesis of a unique couple belongs to the set of the optimizing conditions.

G. SERMONTI (Italy) continued and expanded upon the discussion of speciation. He emphasized the importance of geographical isolation (producing reproductive isolation) rather than genetic rearrangement in the formation of new species. New forms can develop within a range of possibilities determined by constraints of environmental selection, phylogenetic history of parent species, and especially of internal developmental (ontogenetic) constraints. Sermonti pointed out also that ontogenetic differences between species should provide insights into the understanding of their nature; this applies specifically to the ontogenetic divergences between man and the apes. The question was raised whether the emergence of human culture was a gradual or a punctuational phenomenon.

Conclusions

Our present understanding of primate evolution derives from three major sources: the fossil and archeological records, comparative morphology (including chromosomal morphology) and comparative molecular biology. The African fossil record gives evidence of arboreal primates that lived between 35 and 25 million years ago 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 15 and 7 million years ago. *Ramapithecus*, formerly considered to be on the hominid line, is now generally thought more likely to be on the line leading to the orangutans.

The earliest evidence of undisputed bipedal hominids comes from eastern and southern Africa and is dated between 4 and 3 million years ago. This is provided by creatures which had brains the size of living chimpanzees. Indeed a striking trend of subsequent hominid evolution, leading to modern *Homo sapiens*, has been increasing absolute (and relative) brain size, and the development of material culture and language. The earliest stone tools are dated between 2 and 3 million years ago, at least one million years after hominids appeared in the fossil record. A possible explanation for this hiatus is that hominids prior to 2.5-3 million years possibly used unelaborated and perishable material and began later fabricating stone into recognizable tools. During hominid evolution, the interaction between morphological and cultural evolution was a close one.

Comparative morphology 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 million years ago, whereas the orangutan line diverged 10 to 16 million years ago in Asia. These divergence times are fairly consistent with the known fossil record.

Thus, the general outlines of primate and human evolution are becoming clearer, but many aspects remain unresolved — for example, the precise timing of divergences, the genetic relations between fossil and living species, the sequence of morphological evolutionary changes, and the role of the environment in such events as the emergence of bipedalism. These aspects should become better defined with the accumulation of new data from fossil and archeological finds, from comparative morphology and from molecular biological investigations including DNA sequencing and paleo-immunology. A vital issue for ongoing biological research is the relationship between genomic expression, ontogenetic development and adult morphology. Continued investigation into the cultural and social dimensions of hominid evolution should help clarify critical questions such as the interrelations of tool use and manufacture with brain development and the origin of language.

We freely acknowledge that there is room for differences of opinion on such problems as species formation and the mechanisms of evolutionary change. Nonetheless, we are convinced that masses of evidence render the application of the concept of divergent descent to man and the other primates beyond serious dispute.