



## Final Statement of the Working Group on Recent Advances in the Evolution of Primates



A working group of twelve scholars from six countries convened on 24-27 May 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, *Propithecus* 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, focusing 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 1970s, 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, *Australopithecus 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. Bone 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 paleoecology 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 Borne, 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 basis 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 archaeological 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 DNAs of two or more species. Of the approximate 10<sup>9</sup> 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 radio-immunoassay 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 archaeological 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 archaeological 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.