Reflections on a career in human paleontology

Salutations.....

I am very grateful to the Foundation and the Committee for this award for many reasons, but one of them is that it has forced me to look back over my career and to recognize the many important changes that have occurred in human origins research since I was a student.

At the outset, though, I have to tell you that if my life had gone as I'd planned it in my youth I would not be standing here this evening. I had intended to be a fish paleontologist, and my studies at Cambridge in geology and zoology were to that end. I had found fossil fish as a youth and was struck by their beauty and complexity. But an unfortunate encounter with the man in change of fossil fish at the British Museum convinced me that I could not work in that branch of paleontology. The person who had introduced me to him was Kenneth Oakley, a family friend, and the keeper of anthropology at the British Museum. He solved my quandary by showing me a large collection of subfossil lemurs from Madagascar that only been analyzed superficially. And that is how that I switched from wanting to study fossil fish to studying fossil primates. As Oakley himself was not an anatomist, he introduced me to my future academic advisor, John Napier. And so it was that I learned primate and human anatomy, a skill that has since enabled me to earn a livelihood teaching medical students on three continents.

I cannot praise Napier enough. He was a wonderful teacher and a gifted researcher who had the foresight to see that the proper study of fossil primates ought to begin with the study of their living relatives. He invented the field of primate paleobiology. Because of a childhood accident that left him with a deformed leg, he was not able to study living primates in the wild, and although he graciously submitted to being dragged by me along a cold and muddy English beach to be shown the boundary between the Eocene and the Oligocene epochs, finding fossils was not to his liking either. Through Napier's link to Sir Wilfrid Le Gros Clark, the chair of anatomy at Oxford University, he became involved with Louis Leakey. And so as a student I was introduced to hominid fossils from Olduvai Gorge, Tanzania and anthropoid fossils of the early Miocene genus *Proconsul* from Rusinga Island, Kenya.

On a Friday in 1965, Napier told me that there was job available teaching anatomy to medical students in Kampala, Uganda, and that he would give me until Monday to accept the position. I was lucky to have worked in Uganda, Madagascar and Kenya during stable political times and I devoted the time I had on weekends and on vacations to studying the locomotion of living primates, from prosimians to chimpanzees, and to finding new fossil sites. As Napier's urging I began to try, as much as I could, to study extinct animals in the same way that one might study living ones. This meant night-time expeditions to forests and keeping a small colony of primates in my backyard. In the middle 1960s this was a new approach for a paleontologist. It was also a time when many of the inaccessible regions of the world were being opened up because of development, fast and cheaper air travel and the use of four-wheeled drive vehicles. New fossil discoveries were as inevitable as were the new insights from primate paleobiology.

In 1969 I moved to Nairobi, Kenya, to help start up their first medical school. It was here that I linked up with Richard Leakey, the National Museum's young Director.

This collaboration with Richard lasted until he became Director of Wildlife Services for the Kenyan government early this decade. I didn't get to participate much in the exciting expeditions that Richard was carrying out at Lake Turkana because I was teaching medical students for 9 months of the year. I did, however, become involved in the preparation, description and analysis of hominid fossils from Lake Turkana. This was my first personal involvement with hominid fossils and, because I removed the rock from these specimens, I got to know each one intimately. Richard's expeditions on the East Side of Lake Turkana recovered many contemporaneous fossils of robust *Australopithecus* and early *Homo* and were a major addition to the hominid fossil record. Among the many things that these fossils were important for, was the testing of the Single Species Hypothesis that stated that only one species of early hominid would be living at any particular time. We were able to falsify this prevailing theory by finding skulls of *Australopithecus boisei* and *Homo erectus* in the same stratigraphic interval.

I moved to the United States at the invitation of Don Fawcett, the chairman of the anatomy department at Harvard Medical School. In 1972 Fawcett gave a lecture in Nairobi on the structure of the kidney and showed scanning electron micrographs of kidney preparations. This was the first time that I had seen such images and I immediately asked him if I could use such a microscope to study the structure and wear on fossil teeth. He invited me to spend six months teaching in an innovative program in health sciences as a way of getting access to his microscope in Boston. This initial offer eventually led to my being offered a joint position in anthropology and anatomy at Harvard University.

I wanted to study tooth wear for a good reason. I realized that food could leave characteristic marks on the teeth of animals and that these could be used to retrodict the diet of extinct animals. I needed a good modern example in order to show that this method could work. I needed to study the teeth of two species of animal that were related closely enough that their tooth anatomy was similar, that lived in the same place so the effect of soil and climate was controlled for, and that had different diets. I also needed to have a collection of their skulls. This was a difficult sample to get, but a colleague who had studied sympatric species of hyrax on the Serengeti Plain in Tanzania had such a sample. I was able to show by scanning electron micrographs of their teeth that we could easily distinguish between two species one of which ate grass and the other that browsed on leaves. At the same time I gave part of the sample to another colleague that I had met in the United States, Michael Deniro, who was able to show that Carbon isotope ratios in the animals' bones could also distinguish the two diets. This work laid the foundation for chemical and physical methods for determining diets in extinct species, methods that are used extensively in paleontology today.

It is something of an irony that as I no longer worked in Kenya I could spend more time doing field research there. My teaching schedule now left me with time to go in the field with Richard Leakey and we carried out a series of expeditions to late Miocene deposits in the early 1980s that were successful from the point of vertebrate paleontology, and also led to the discovery of interesting new fossil anthropoids. These showed us that the diversity of large anthropoids in the middle Miocene was much greater than we had suspected. We had even greater success with expeditions to PlioPleistocene deposits later in the decade.

I went to Rusinga Island in 1984 for a curious reason. A British paleontologist had studied the Miocene fossil pigs that Louis Leakey had collected from Rusinga Island in Kenya. When he returned the collection to Nairobi he also returned a primate foot skeleton that had been mistakenly put with the pigs. This turned out to be from the same *Proconsul* individual that John Napier had studied in the 1950s and that were thought to come from an infilled pothole. We then found other parts of this skeleton in the museum that had been misidentified as other animals. This, in turn, led us to think that Louis Leakey might have left even more on the site. In 1984 we rediscovered the site and cleaned up the area where Leakey had worked in 1950. We immediately found more of the skeleton that had been sitting there for over 30 years. After searching all the possible rocks from the infilled "pothole" we tackled the problem of the formation of it. We found that, rather than being an infilled pothole in an ancient river bed, this was the infilling of a hollow tree trunk. All the vertebrate skeletons in the infilling were animals that had used it as a refuge or that were carried in by predators. The juvenile *Proconsul* was one of these, carried in by a carnivore. We know now that there are several of these infilled Miocene trees that have bones in them that are still standing on Rusinga Island. It is quite possible that other fossil primates are still encased in these 18 million year old vertical tombs!

One of my colleagues discovered another *Proconsul* site on Rusinga Island while we were working on the fossil trees. We excavated at this new site for two seasons and recovered parts of the skeletons of ten *Proconsul* individuals, from adults to babies. Different teams of researchers have been analyzing these bones and teeth since then and have made significant strides in understanding the paleobiology of this early anthropoid. The last of these to be published involved the determination of the life-history of the species by detailed analysis of tooth development. All calcifying organisms do so with a daily rhythm, and primates are no exception. A detailed record of daily development is hidden in the enamel of any primate. We deciphered the record in *Proconsul* by sectioning one permanent and one deciduous set of teeth and by the use of confocal microscopy. Although an early anthropoid, the rate of maturation was rather like that of living macaque species. This species of Proconsul became sexually mature at about 6 years.

Later in 1984 Richard Leakey and I went to the west side of Lake Turkana, where Kamoya Kimeu had found a small piece of *Homo erectus* skull in 1.53 million year old sediments near the Nariokotome River. This small piece of skull was the surface manifestation of one of the most complete early hominids ever found, the Nariokotome *Homo erectus* skeleton. The National Geographic Society gave us money for 5 years to excavate this specimen. When we had finished in 1989 we had moved 1000 tons of sediment by hand and wheelbarrow and had washed all of the excavated sediment in Lake Turkana through fine sieves. I assembled a team of researchers to put together an account of this skeleton and the environment in which it lived. This team, mostly made up of younger researchers, put together a first analysis of the skeleton that was published in 1993. We learned more from that one skeleton than from all the dozens of other fragments of the species that had ever been found.

The skeleton was remarkably like modern humans in most fundamentals apart from brain size. We found that these early members of our own genus were physiologically adapted to dealing with the high heat load of life in the open on the equator. They had a slender, elongated body shape which provided a large surface area for sweating and cooling, just like those modern people who live in such conditions today. This was in contrast to the body shape in earlier, antecedent *Australopithecus* species. We also found that early *Homo erectus* individuals were large and that previous determinations of body size and stature based on fragments of limb bones were underestimates. This suggests that many modern humans are smaller than our distant ancestors. The most interesting finding, perhaps, was that of Ann MacLarnon, who studied the neural canal of the vertebrae of this skeleton. She showed that the upper part of the spinal cord was narrower than those of modern humans and only the same size as those of living apes. She hypothesized that this was because the individual lacked the fine motor control over the muscles of the abdomen and ribcage that allows modern humans to make sentences when speaking. This was some the first new evidence for some time in the debate on the origins of human language.

Science and Art are different in many ways, but one of the most important is that observations and ideas in Science are always being corrected. This is how progress is made, with old observations being shown to be wrong and old ideas corrected in the light of new observations. One of my colleagues, Bruce Latimer, has recently shown that our observations on the vertebral column of the Nariokotome individual were incomplete. What we missed initially was that this individual had suffered damage during childhood to the intervertebral disc between his last and penultimate lumbar vertebrae. This would have given him a mild scoliosis - a lateral curvature to the spine - and this in turn would have led to compensatory changes in his upper spine. We assessed the importance of those changes wrongly because they produced a primitive, chimpanzee-like morphology. Instead of recognizing these features as the response to an injury we thought they were primitive morphological retentions. We are still debating whether or not this injury would have affected the cervical neural canal size, but at the least this casts suspicion on the claims that this individual had a normal narrow neural canal.

In 1985 we were still exploring the sediments to the west of Lake Turkana when I discovered the cranium of an early member of the robust *Australopithecus* lineage. This skull, called the Black Skull because of its manganese dioxide staining, is about 2.5 million years old and it spelled trouble for the simple phylogenetic schemes of the times and required a re-thinking of hominid phylogeny. It was part of the same species that had been named by Professors Camille Arambourg and Yves Coppens in 1967 as *Paraustralopithecus aethiopicus* for an toothless lower jaw from sediments about same age in the Omo deposits, some 100 kilometers to the north. The evolution of this separate lineage of big-toothed bipedal hominids has been a preoccupation of mine, and we have made big advances in understanding it, but there is still a lot that needs to be learned about these bizarre extinct cousins of ours.

My present research involves a collaboration with several researchers in different disciplines. My earliest work involved trying to work out, by analogy with the behavior and anatomy of living primates and by biomechanics, how extinct species moved and what their habitual postures were. But having done that I had no test of whether or not I was correct. My colleague Fred Spoor, from University College London, has demonstrated that, once the effects of body size are removed, the semicircular canals of primates are tuned to the speed of their locomotion. This now gives us an independent method to test our earlier ideas about the locomotion of extinct primates. But studying the semicircular canals of fossil skulls is not an easy task and we will have to use an industrial micro CT machine in Texas to make the images required. We have already tested some old hypotheses on a small sample of fossil primate skulls. Some have survived the test and others have not. In the end we will be more certain about the evolution of the primate locomotor system.

In summary, I have been lucky in being able to do field work in relatively stable times in Africa. I have also been fortunate to work with gifted colleagues and students. The field of paleoanthropology has itself evolved in the last half of this century from an occupation involving a few individual academics working in relative isolation to one in which teams of researchers with many differing skills work together to solve larger questions.

The science of human origins is still developing. There is now a revolution in the biological sciences brought about by molecular biology and paleoanthropology will play its part in this revolution. It is becoming easier today to find the genes responsible for our individual traits. One of my own students is trying to bring paleoanthopology and modern developmental genetics together by looking for the genes responsible for tooth development in primates. She wants to understand the genetic basis for the different shapes of primate teeth. Once she has identified the genes or groups of genes involved we will then be able to look back in the primate and human fossil record to see when they were selected for and in which order. This in turn will give us a modern understanding of the genetic mechanisms underlying our own morphology and lead to further hypotheses regarding the selective advantages of some of our important features. Human origins research is, then, at a wonderfully integrative stage of its development and I am happy and privileged that I can take part in it.