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Hominid Evolution

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I. Introduction

Man's relationship with nature, his place in the universe, and the manner of his origin have been topics of speculation and controversy throughout recorded history. Religion, folklore, and science have dealt with these topics in a variety of ways, posing explanations and answers which are satisfying to some and inadequate to others. Accepting the premise that religion encompasses matters of faith, whereas science is the domain of that which is demonstrable, this unit provides methods for familiarizing the student with recent and contemporary scientific thinking about human origins.

From the discovery of the Taungs baby in South Africa in 1924 and its subsequent description by Raymond Dart, to the 1979 announcements of the new species *Australopithecus afarensis,* the new hybrid primate siabon, the discoveries of 3.8 millionyearold fossil hominid footprints, and of the earliest known fossil anthropoids, there has been a steady progression of major finds, new interpretations, and revisions of man's thinking about his origins. Human evolution is a subject attracting as much attention and publicity today as at any time in the past. Our understanding of the last 15 million years of hominid evolution is vastly more complete than it was half a century ago. The term 'hominid' is used here to denote man and his immediate ancestors or nearancestors.

Biology textbooks frequently relegate topics in evolution to the last chapters of the book, much the way that organic chemistry used to be an addendum to chemistry textbooks. This is unfortunate when one considers that evolution is one of the most substantiated of theories in the biological sciences, and that it is also one of the major unifying theories of biology. Evolution introduces a fourth, temporal dimension to biology. It is that aspect of the science which reminds us that we presently represent a minuscule fraction of biological history.

The diverse forms of life on earth today—between one million and two million different species—exploit their surroundings in a multiplicity of ways, while at the same time being limited and partially fixed by their surroundings. Today's forms of life are the products—and it must be emphasized, not the endproducts—of an extremely long evolutionary process. Despite our increased knowledge of the processes of evolution, teaching these processes is one of the most difficult aspects of any biology class. The suggestion that man has evolved from earlier, different forms of life is one which is easily misunderstood and frequently dismissed by our students as beyond belief. By presenting much of the evidence for human evolution and having the student participate in some of the activities of a paleontologist, it is hoped that the student will be in a better position to draw his own conclusions, Consequently, laboratory activities such as examining animal bones, preparing plaster casts, and working with photographs of important hominid fossils are a major part of this unit.

Among the objectives of the unit are the following:

1. to present methods for better understanding the magnitude of geological time;
2. to familiarize the student with basic characteristics of hominid forms;
3. to consider some of the interdisciplinary methods for studying human origins;
4. to consider the relationship between morphology (structure) and function, as applied to hominid characteristics;
5. to familiarize the student with the modern consensus ideas of human evolution, including consideration of recognized species of hominids and their discovery sites;
6. to present the idea that scientific data are frequently interpreted differently and that scientific models change.

The unit is intended for Biology, Advanced Biology, and Anthropology students who have had some background in the study of animal diversity and evolution. It can be adapted for use in other science classes.

II. The Magnitude of Geological Time

Because evolution is a subject that involves the passage of time, it is essential that the student have an understanding of the magnitude of geological time. Humans measure time on the basis of years and, at most, decades. The average lifespan of Western man is approximately seven decades. More immediate events in our lifetimes are measured in days, hours, and minutes, The concept “one million” is very much beyond our full comprehension, and yet one million years is an extremely short period of time in geological terms. The earliest known forms of life date back three thousand million years, “Molecular fossils” which resemble living cells have recently been found in Greenland, and they have been estimated to be 3.8 billion years old. Mammalian evolution has been taking place for 200 million years, and there are ancestral primates known to have lived 70 million years ago. How, then, does one acquire some appreciation for the magnitude of time?

In the 1950s a book entitled *Cosmic View: The Universe in Forty Jumps* took a very interesting approach to the study of space, a concept equally as difficult to grasp as that of time. Beginning with a drawing of a young girl sitting in a rocking chair, the author moved a step at a time, by powers of ten, outward from the girl, and then inward. Each succeeding drawing took the observer ten times farther away from, or closer to the girl. Within the first few jumps outward, the observer realizes that the girl is sitting in a school yard, that the school is located in a farming region, that the farmlands are in western Europe, that the earth’s northern hemisphere is being represented. Each jump of a factor of ten develops a feeling for the magnitude of self, region, continent, hemisphere, earth, solar system, galaxy, and known expanse of the universe. In the reverse direction, moving from our most familiar frame of reference to smaller objects, the imaginary camera, now installed on a microscope rather than a telescope, focuses on skin tissue, cells, cellular organelles, molecules, atoms, and subatomic particles. Forty different frames of reference were required in this book to span the magnitude of the universe known to man.

More recently and in a similar approach, the astronomer and writer Carl Sagan has refined an effective method for the study of time. Taking the history of the universe from the time of the Big Bang, currently estimated as having occurred fifteen billion years ago, up to the present, and condensing this time into one imaginary calendar year, January 1 through December 31, one can develop a “cosmic calendar.” January 1 marks the occurrence of the Big Bang, that “moment” when all of the coalesced matter of the universe exploded outward and began its migration away from the center. The last tick of this geological clock, on December 31 as 11:59.59 passes by, marks the approach to the present. One can then mark notable events on this calendar, such as the formation of our solar system, the cooling of the earth’s crust, the first appearance of life on earth, and the appearance of man’s progenitors. Such a calendar is easily adapted for the study of hominid evolution.

In preparing his own cosmic calendar, the student learns that life on earth has had an enormous amount of time in which to change. With an estimated 4.5 billion year age of the earth (early September on our calendar), and with life first appearing at least 3 billion years ago (the first week in October), one begins to get the feeling that it would be far less likely that life would remain continuous and unchanged for such vast periods of time. At the same time, one realizes that our residence on this planet has been relatively brief: the first m~mals appear on the cosmic calendar on December 26, and the first primates do not make an appearance until December 29* Those forms that we call hominids appear late in the day on December 31. Our calendar. which is more detailed for the final days and hours of December, is developed to reflect the appearance of life forms now extinct: early pongids (apes); dryopithecids (Miocene apes); ramapithecids (the first ape like inhabitants of open grasslands); australopithecids (close relatives of *Homo*). *Homo sapiens* (modern man) appears at approximately 11:59 p.m. On the last day of this imaginary year. Although we can never fully grasp the magnitude of vast periods of time, the calendar does give some perspective on the length of time during which evolutionary change has taken place.

It is also helpful to look at generation time in comparison with geological time. Different organisms are capable of reproducing at different rates. Bacteria growing under optimal conditions can reproduce asexually every 20 minutes. If it were possible for bacteria to divide at this maximum rate over an extended period of time, 72 generations of bacteria would be produced in 24 hours. More than 26,000 generations would follow in the first year. Obviously, all bacteria don’t reproduce unchecked, but their overall generation time is very short.

Generation time in humans varies widely, with the capability for reproduction ranging from 12 to 18 years. Assuming an average generation time of 20 years, there have been 10 generations that intervene between us and time of the American Revolution; 100 generations since the time of Jesus; at least 15,000 generations since Peking Man; 50,000 generations in the past 1 million years. Similarly, each of us has had 210=1024 ancestors since the American Revolution; 250,000 ancestors since 1 million years B.P. That is a lot of generations and a lot of ancestors. (B.P. = before present).

The geological epochs during which hominids and nearhominids have evolved are the Miocene, Pliocene, and Pleistocene Epochs. These epochs are referred to in Section IV of this narrative, dealing with the fossil record.

The Miocene spans the period of time from 25 million to 12 million years B.P.* A number of ape species were present in Africa, southern Europe and Asia during the Miocene, including the great ape *Dryopithecus* and the lesser ape *Limnopithecus* . (See slides.)

During the Pliocene Epoch, approximately 12 million to 3 million years ago, tropical forests of the Old World increasingly gave way to open grasslands and savannas. The first arboreal/terrestrial primates to exploit these habitats were the ramapithecines, including *Kenyapithecus* , *Gigantopithecus* , and *Ramapithecus* . Toward the end of the Pliocene the first hominids, the australopithecine, appeared in East Africa and South Africa. The Pleistocene Epoch, 3 million to 10,000 years ago, was characterized by great changes in climate and by extensive glaciation. A number of mammals, including the once diverse hominid lines, became extinct. One hominid line, that of man, emerged.

*The symbol is used for “approximately” throughout this paper.

III. Methods for Studying Hominid Evolution

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1. Comparative morphology

Natural relationships among organisms can be fairly well determined by comparing their various structural features. Modern forms of life have been classified into related taxonomic categories (genera, families, etc.) based on similarities in foot structure, teeth, skull shape, method of reproduction, type of locomotion, and a number of other characteristics. Among the modern primates, for example, the prosimians, Old World monkeys, New World monkeys, apes, and man are recognized as distinct groups.

Comparative morphology is used in studying extinct forms of life whose skeletal remains have been recovered. Important similarities suggest relationships among earlier species and link some of them with present species. Scientists can develop histories of evolving species (phylogenies).

Some of the morphological features which help to classify hominids

are:

> *cranial morphology*— height of the cranial vault; cranial capacity; presence of a sagittal crest on top of the skull (for attachment of strong chewing muscles); presence of brow ridges (for muscle attachment); degree of facial recession; position of the foremen ma B um (the opening at the base of the skull through which the spinal cord passes).
> *dental characteristics*— size of the cheek teeth (premolars and molars) in relation to the front teeth (incisors and canines); number of cusps on the molars; shape of the dental arcade (Ushaped, Vshaped, or parabolic.)
> *postcranial characteristics*— the intermembral index (the ratio of the length of the arms to the length of the legs); shape of the pelvis (the entire complex of characteristics that determines the method of locomotion—brachiation, knucklewalking, or bipedalism); manual dexterity (ability to use the power grip (first clenched on an object) and the precision grip (thumb and opposing forefinger— the OK sign.

2. Fossilization

The hominid fossils that have been recovered in Africa, Europe, and Asia over the past 120 years are the products of mineralization. This natural process has occurred by the seeping of minerals into the hard tissues of animals or plants which had been fortuitously covered by sediment, Fossils are faithful copies of onceliving organisms. When an animal skeleton is fossilized, the bone material is completely replaced by minerals.

Until fairly recently, very few hominid fossils had been located, and it could be said that all such fossils collected together would be held by one goodsized table. A number of continuing expeditions for fossils in wellknown sites in the Old World have produced greatly expanded collections that have increased our knowledge of hominid evolutionary history. There remain significant gaps in the fossil record, however. Postcranial remains, for example, fossilized ribs and vertebrae, arm and leg bones, hand and foot bones, and pelvises, are scarce when compared to the number of tooth and skull fragments that have been found. The postcranial bones are smaller and softer and tend to disintegrate (or be scavenged) much more readily than the hard bones of the head.

In terms of a temporal record of hominid evolution, there is a serious gap in our knowledge; we know little or nothing of the period from 8 million to 4 million years ago, No wellpreserved and welldocumented hominid fossils have been found from this four millionyear span of time. As this may well be the period during which apes and hominids diverged from a common parent stock, future discoveries from this age will be particularly important.

Evidence of earlier types of life can also come in the form of imprints or casts. The track left by a crawling worm can be fossilized, as can footprints, such as the wellknown dinosaur tracks of the Connecticut River Valley. The recent announcement by Mary Leakey of 3.6 million year old hominid tracks represents an important new way of learning about hominid structure and functional adaptation.

Some hominid skulls have been found with associated natural endocasts. These formations are the result of material filling the skull and becoming part of the enveloping rock matrix. An example of such an accurate copy of the inside of the skull is the Taungs baby, which lacked the back portion of the skull but did have a well preserved endocast, showing how large the skull was.

3. Absolute and Relative Dating

The age of one fossil with respect to another can be determined by one of the methods of relative dating. A principle of geology is that sedimentary or volcanic formations at an undisturbed site are increasingly older as one goes further down in examining the different layers. The most recent layers of rock in a geological formation are at the top. Consequently, a fossil located in a layer of sediment is of an earlier age than one found in the layer above. It has been found that two sites separated by considerable distances may have some common sequences of rock layers. These comparable layers are assigned the same approximate ages. By considering two or more sites together, an expanded cross section of the earth’s layers is seen. Fairly complete chronological histories of a geological region are thus obtained.

The same types of fossil plants and animals are often found in comparable layers at two sites. If the rock layers at one of the sites are not easily distinguishable, comparisons of the fossils at each site can help determine the correct layer. Such floral and faunal comparisons help to date hominid fossils found in poorly defined layers or in a stratigraphy which is subsequently destroyed. The limestone deposits of South Africa, for example, have been destroyed by quarrying or are not suited for absolute dating techniques. Approximate ages of these deposits have been obtained by making faunal comparisons with the welldated deposits of sites in East Africa.

Absolute dating assigns a specific age to a layer of rock or a fossil. These techniques involve an examination of the levels of radioactivity in rock samples. Organic remains, volcanic material, and sedimentary rock contain unstable isotopes of elements that undergo continual decay. The relative amounts of the radioactive isotopes present in the organism when it was alive, in the lava and ash when they were released from the volcano, and in the sediment when it was laid down are known. Also known are the rates at which the various isotopes decay to form more stable products. Potassium Argon dating is the technique best applied to early hominid and pongid fossils, which are several hundred thousand to more than 10 million years old. An unstable form of Potassium, K40, which is present in volcanic ash, breaks down to form Argon40. The halflife (tt = the amount of time it takes for one half of the unstable atoms present in the original material to decay) of K40 is 1.3 billion years. KAr dates reflect a degree of uncertainty of this process by showing a range of years. Thus, the ER1470 skull described by Richard Leakey was dated at 2.50=0.25 million years before present.

4. Endocranial casts and microwear of teeth

The process of fossilization sometimes produces natural endocranial casts which conform to the inner contours of the skull. Synthetic polymer casts can also be prepared, in a technique developed by Ralph Holloway. Holloway has prepared casts of six South African australopithecine skulls, as well as endocasts for East African australopithecine, *Homo habilis* from Olduvai, and the 1470 *Homo habilis* from Koobi Fora. The casts give accurate measurements of cranial capacity, and outlines of blood vessels of the membrane surrounding the brain. The size of the major subdivisions of the brain—socalled gross brain morphology—can be determined.

Holloway concludes that *Australopithecus* had a brain which was essentially human in organization and that its brain was in the same general proportion to the size of its body as is ours. His data would tend to support the idea that a humanlike brain was present in hominids 3 million years ago, even though rapid expansion of the brain took place much more recently.

Within the last year another technique for studying hominids has been developed. Alan Walker is studying the microwear of teeth of living and extinct mammals. He uses fossil and modern teeth to prepare epoxy replicas which are then examined under the scanning electron microscope for microscopic wear patterns. The scratches and pits on teeth provide clues as to the diets of each organism. Grazing animals, which eat grasses, have teeth with a number of microscopic pits or abrasions on their surfaces. Grasses have large quantities of silica crystals in their cells which scratch tooth enamel. Browsing animals feed on the leaves, branches and fruits of trees and bushes. These plant materials have fewer silica crystals in their cells, and a more finely polished tooth surface results. Omnivorous animals, eating meats as well as plant material, scratch their teeth heavily when biting into bone.

By comparing tooth wear for mammals whose dietary habits are known with wear on teeth of extinct hominids, the diets of early hominids can be determined. Walker's initial studies show that *Homo erectus* was the first omnivorous hominid, and that the australopithecines and *Homo habilis* were herbivorous, principally eating hard fruits. This would require that early hominids fed in forested areas, rather than exploiting open grasslands, as is generally believed.

5. Molecular evolution

Paleontologists assume that the greater the differences in morphology between two species, the more remote in time is the ancestor common to both species. Molecular evolutionists argue that this is equally true for the genetic and protein differences between species. If two types of life are very different in terms of their protein structure and genetic makeup (when comparing the same proteins and genes), then they have evolved separately for a very long time. A number of scientists are now studying evolution at the molecular level. Among them are biochemists Vincent Sarich and Allan Wilson, who are studying blood proteins in a variety of living organisms. Their approach to the study of evolution is advantageous in that they can quantify their date and they can compare forms of life that are extremely different morphologically.

One of the assumptions made by molecular evolutionists is that gene mutations and consequent protein changes occur at a relatively steady rate, much as radioactive isotopes experience constant decay. If this is true, then evolution has a builtin molecular clock, The ticks of the clock are the substitutions in nucleic acid base pairs or the amino acid replacements in proteins. Using the recently perfected methods of hybridization, rapid sequencing, and recombinant DNA work, the nucleic acids and proteins of different organisms can be compared. The number of amino acid differences in the blood albumin of two different species, for example, can be determined, and the duration of evolutionary time needed to achieve those differences can be calculated. By using the minimum number of gene mutations or amino acid substitutions needed to get two different proteins, the time of divergence of the two species is found. Different molecules are found to evolve at different rates. If one is able to determine the correct rate of evolution for a given molecule, this serves as a new indicator of the time of species divergence.

Data collected so far indicate that there are strong molecular similarities among humans, chimpanzees, and gorillas, and that these two great apes are genetically as similar to humans as they are to each other. The time that hominids diverged from the apes is set at approximately 5 million years ago. This is much earlier than the 14 to 8 million year divergence time set by paleontological studies. With the present relegation of *Ramapithecus* to nonhominid status, however, the earliest known hominid is now 3.8 million years old. The molecular clock is now playing a bigger part in evolutionary theory. Some researchers regard it as a sloppy clock, but one worth referring to.

IV. The Fossil Record—Key Discoveries of this Century

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1. *Australopithecus africanus* (The South African apeman)

In 1924 at a limestone quarry at Taungs, Cape Province, South Africa, workers exposed what has been described as the greatest fossil find ever made. The discovery consisted of two interconnecting rock fragments which, on examination revealed the forward part of a skull, and much of the lower jaw of a previously unknown form. A natural endocast of the braincase also made up part of the find. Found by chance during mining operations for the Northern Lime Company, the humanlike character of the skull was recognized by the quarry foreman in charge of the blasting, M. deBruyn. The two rock fragments were eventually delivered to Dr. Raymond Dart, a physician and professor of anatomy at Witwatersrand University in nearby Johannesburg.

Raymond Dart spent more than four years working on the fossil skull. He eventually freed the lower jaw from the enclosing rock matrix, exposing the surfaces of a complete set of milk teeth, as well as the first permanent set of molar teeth. The molars were just in the process of erupting, suggesting that the ancient owner of the **s** kull was a young child of about five or six years.

The Taungs child, as it came to be known, showed characteristics which contradicted thenprevalent notions of the appearance of man's early ancestors. With a relatively large jaw and a brain capacity estimated at 405cc., or midway between that of the common chimpanzee and gorilla of today, the Taungs child appeared apelike to most contemporary scientists. What seemed contradictory was that the fossil teeth were clearly human in appearance, though they were larger than the teeth of modern man at the same age. The creature was not large brained and largejawed, as would have been expected.

Dart's description of Taungs, which he named *Australopithecus africanus* —the South African apeman—and his subsequent speculation about Taungs' humanlike brain structure and probable tool use were generally regarded as fallacious notions by his colleagues. Taungs was explained away as an aberrant and pathogenic form of man. Not until related finds were made at Sterkfontein, Swartkrans, Kromdraai, and Makapansgat in nearby regions of South Africa, by Robert Broom and John Robinson, was Taungs accepted as an important PlioPleistocene find.

The site of the fossil discovery at Taungs has long been destroyed by mining operations. Because of the absence of material suitable for absolute dating, the age of *Australopithecus africanus* from Taungs must be regarded as unknown. Few fossil faunal remains were found in association with the skull. There are no stone tools from this site. By comparing the Taungs skull with A. africanus remains subsequently found at the other South African sites, however, the age of the Taungs infant is now roughly estimated at 1.8—0.8 million years B. P. which makes it a latesurviving member of the species. This is in spite of the fact that Taungs is the type specimen for *Australopithecus africanus* .

Australopithecus africanus was probably an omnivorous form, feeding on plant materials such as seeds, nuts, berries, and roots, as well as on occasional insects and other small animals. This is the species of australopithecine described as gracile (slight), with a moderatelysized jaw and no prominent bony ridges on the skull. It has recently been described as o *ccurring in East Africa, as well. Australopithecus africanus* specimens thus far found suggest that the species remained relatively unchanged in Africa for more than 2 million years, from approximately 3 million to perhaps less than 1 million years ago.

2. *Homo erectus* (*Sinanthropus pekinensis* —Chinese man from Peking, or Peking Man)

The Taungs baby was discovered by a quarryman and it was fortuitously turned over to Raymond Dart, an anatomist who was willing to discard prevalent notions of how early hominids must have appeared. Circumstances for the discovery of *Homo erectus* fossils in China were considerably more involved.

Traditional peasant drugstores in China were known to carry "dragon bones," in jars of fluid. These dragon bones were rocklike bones which, when ground to a powder, were used for medicinal purposes. They were often, in fact, the fossilized remains of prehistoric and extinct forms of life. Scientists in this century have at times made pilgrimages to the Chinese drugstores, looking for fossil hominid remains. By asking questions of the local people, the sources of the fossils have sometimes been determined. In this fashion, the fossilbearing limestone quarries of Chou Kou Tien, near Peiping, China, were discovered by the scientific community.

In 1926 two obvious human teeth were discovered at Chou Kou Tien. The discoveries were announced by Dr. J. Andersson, a Swedish geologist, and by Davidson Black, a Canadian who was an anatomy professor at Peking

Union Medical College (Rockefeller Medical College of Peiping). The following year an international team was organized to conduct a thorough dig of what proved to be a large ancient cave, which had gradually filled in with sediment. Key scientists involved in the project were Black, who died in 1934, his successor Franz Weidenreich, a German scientist, Pei Wenchung (W. C. Pei) of China, and Pere Teilhard de Chardin of France.

The fossil teeth were assigned to a new generic category, *Sinanthropus* . With the specific name *pekinensis* , these fossils were known as Chinese Man from Peking. By 1928 the skull of a child was unearthed at Chou Kou. Tien, and in a twoday period in November, 1936, three more skulls of Peking Man were found. During ten years of digging, blasting out, and sifting rock, from 1927 until 1937, remains of 30 to 40 individuals were unearthed. Although few postcranial bones were found, the excavation turned up individual teeth, mandibles, and a total of five wellpreserved skulls. Strong evidence for use of fire (charcoal fragments) and for tool use (pieces of quartz not native to the area) was also obtained.

The advent of World War II brought a halt to the fossil excavations. Scientific study and political realities clashed headon in 1941, when Japanese troops invaded and occupied China. The Peking Man fossils were crated up with the intention of sending them to the United States for safekeeping, but in December of 1941, shortly after the United States entered the war, it became known that the fossils were lost. Though the fate of the fossils has to the present remained a mystery, in recent years the nature of their disappearance has become more clearly understood. During the Japanese occupation of China, Japanese troops confiscated the boxed fossils, while imprisoning the U.S. Marines who were responsible for safekeeping of the fossils. In the course of moves from one prison camp to another, it is likely that most of the fossils were discarded by the Japanese troops as being of no value, At the conclusion of the war, a few of the less important remains were recovered in Tokyo, suggesting to some people that the possibility still exists that other Peking Man remains will again be recovered.

Prior to the outbreak of the war, a number of excellent casts were made of the Peking skulls; they, along with drawings and very complete descriptions of the finds, were brought to America by Weidenreich. In the postwar period, excavations at Chou.Kou.Tien began again, and new discoveries have been made. Consequently, although most of the original material has been lost, valuable information does exist about the fossils.

Peking Man is characterized by a large cranial capacity, 9001200 cc. Along with the evidence for his use of tools and fire, the large brain size suggests that Peking Man was indeed an earlier form of human. The Chou Kou.Tien fossils are of the same type as some fossils found in 1891 in Java by Eugene Dubois, a Dutch physician. Dubois had set out to discover the remains of early humans and within a year had succeeded in locating a skull cap and thigh bone near the Solo River in central Java. They were given the name *Pithecanthropus erectus* , and they were more commonly known as belonging to Java Man. Java Man and Peking Man have since been reclassified as *Homo erectus* , using Dubois' species name but recognizing that the remains are of an earlier form of human. Other *Homo erectus* remains have more recently been discovered in East Africa at Olduvai and Lake Turkana. Louis Leakey's Olduvai specimen, known as O.H. (Olduvai Hominid) 9, was found in association with stone handaxes, and it is dated at 490,000 years B.P. The skull found by Richard Leakey at Koobi Fora, Lake Turkana, Kenya, labeled as KNMER (Kenya National MuseumEastRudolph) 3733, is an extremely wellpreserved specimen having a cranial capacity of 800 cc. This skull has been dated to 1.6 million years B.P., considerably earlier than any previous finds. Current estimates for the age of Peking Man indicate that he lived 500,000 to 300,000 years ago, with the younger age being more likely. Java Man is judged to be several hundred thousand years older.

Homo erectus was a wideranging species, found throughout parts of Africa and Asia, a species which persisted for perhaps 1 1/2 million years. In addition to a cranial capacity about twothirds modern size, the species is characterized by a very thick skull which is flattened in mandible, and large teeth. The postcranial skeleton is quite similar to that of modern man, with a fairly robust pelvis. *Homo erectus* may have been as tall as 5 feet, weighing perhaps 175 pounds.

3. *Ramapithecus punjabicus* (Rama's ape)

While the scientific community was regarding Dart's South African apeman with considerable skepticism and sharing the public enthusiasm for the ongoing discoveries near Peking, a Yale University graduate student named G. Edward Lewis was searching elsewhere in Asia for fossil hominoids. A paleontologist for the Yale North India Expedition examining the Simla Hills badlands, Lewis collected in 1932 a series of fossils including a right maxilla with premolar, molar, and portions of incisor and canine teeth intact. This specimen, numbered YPM (Yale Peabody Museum) 13799 and presently housed with the Peabody collection in New Haven, was assigned the name *Ramapithecus brevirostris* (Rama's shortspouted ape) by Lewis. Rama is a mythological prince in an Indian epic poem. The species name has subsequently been changed to *punjabicus* , a name appearing earlier in the literature describing similar fossil forms. YPM 13799, which may well have been purchased by Lewis in India, is the type maxilla specimen for *Ramapithecus* . It shows that *Ramapithecus* had reduced canines and incisors, cheek teeth with thickened enamel, and that it probably possessed a short face, all characteristics found in the family of man, Hominidae.

A number of additional ramapithecine fossils have since been described. In 1961, Louis Leakey discovered 14millionyearold fragments of two maxilla and a lower molar of a form he named *Kenyapithecus wickerii* , after Kenya Colony and the man who first located the site at Fort Ternan, Kenya, where the fossils were unearthed, Fred Wicker. In the 1960's Elwyn Simons and David Pilbeam, both then of Yale University, examined a number of fossil specimens housed in museums around the world, and they reclassified approximately two dozen fragments as belonging to the ramapithecines. Their work suggested that *Ramapithecus* , a likely descendant of the Myocene ape *Dryopithecus* , was the earliest known ancestor of man, and that it represented the first evolutionary steps away from the pongid line.

During the 60s and 70s, Pilbeam led expeditions to the Siwalik Hills badlands of northern Pakistan, searching for further ramapithecine remains. In March, 1975 and January, 1976 team members made surface recoveries of four bone fragments which fit together to form the most complete mandible yet recovered. The mandible shows that *Ramapithecus* did not have a parabolic, human like dental arcade, as originally thought, but rather a Vshaped, more apelike arcade. Though the shape of the arcade is not now regarded as one of the more anatomically important characters, *Ramapithecus* is no longer granted the high status that it once received. Pilbeam now favors consideration of four major groups, the dryopithecids, ramapithecids, pongids, and hominids, and he avoids models of phylogeny that suggest direct linear descent of one fossil form from another.

Although numerous fossil fragments of ramapithecines have now been recovered from parts of Hungary, Turkey, Greece, India, Pakistan, and East Africa, skull fragments are lacking from the known record, and postcranial remains are all but unknown. The ramapithecines are now dated to 148 million years B.P. It has been suggested that *Ramapithecus* was a bipedal creature, and it is not unreasonable to assume that some form of erect feeding posture was used, both arboreally and terrestrially. More sophisticated use of the hands would be a consequence of such bipedal behavior. Conclusive interpretations of the appearance and significance of *Ramapithecus* await more complete fossil discoveries.

4. *Australopithecus robustus* (Paranthropus robustus—large ape akin to man)

One of the few supporters of Raymond Dart and his conclusions about the significance of the Taungs skull, *Australopithecus africanus* , was Dr. Robert Broom, a paleontologist who in 1936, at the age of 70, determined to locate an adult skull of an australopithecine. Broom felt that the limestone deposits of the Transvaal region of South Africa, some 200 miles northeast of Taungs, were possible sites of fossil manapes. He alerted the quarryman at Sterkfontein limeworks, G. W. Barlow, to the importance of looking for manlike remains. In July of that year, Barlow did present Broom with a braincast of a primitive hominid form, and an extensive search the following day turned up most of the rest of the skull, clearly similar to Dart's find. Broom named the specimen *Australopithecus transvaalensis* , thinking that there were several basic structural differences meriting a separate species classification. This skull of a gracile australopithecine has since been reassigned to *Australopithecus africanus* . A number of other australopithecine finds were made at Sterkfontein during 1937 and 1938, making the original Taungs find a much more believable one.

In June, 1938 at a farm in Kromdraai, within two miles of Sterkfontein, Broom made another significant find. The newly discovered material, catalogued as TM1517, consisted of the skull, teeth, and some postcranial bones from a more robust, largerbodied type of australopithecine. As with the original Sterkfontein material, the initial discovery of these fossilized bones was made not by Broom but by a nonscientist. Quarry manager Barlow had brought Broom a primitive palate and molar tooth, which he had obtained from a local schoolboy, Gert Terblanche. Fresh break marks on toothed areas convinced Broom that additional portions of the skull were to be recovered. He went to the new location and traced the boy to his home, finally locating him at school. "I naturally went to the school, and found the boy with four of what are perhaps the most valuable teeth in the world in his trouser pocket.''1 At the principal's invitation, Broom delivered a lecture on bones and fossil digging to the teachers and students at the school, and upon school dismissal he and the boy visited the hillside at Kromdraai where the palate had been found. The boy delivered another sizable piece of the skull to Broom and through considerable searching and sifting they eventually located much of the rest of the skull. Broom bought the fossils from young Terblanche.

The new skull was given the name *Paranthropus robustus* , reflecting his opinion that it was significantly different from *Australopithecus* as to merit a new generic classification. Originally considered to be much older than the Sterkfontein fossils, the Kromdraai skull is now regarded as being younger, approximately 2.5 to 2.0 million years old. There has been much disagreement as to how old the South African australopithecines are, owing to the absence of good datable material and to changing techniques for absolute dating. Relative dating, particularly fossil faunal comparisons with sites in East Africa, indicate that Sterkfontein is 3.0 to 2.5 million years old.

Five to six individuals were eventually found at Kromdraai. These South African hominids were larger than *Australopithecus africanus* . having a cranial capacity of 500 to 550 cc., as compared with 450 to 550 for the more gracile forms. The molars and premolars are larger, as compared with the incisor teeth, than in *africanus* . The robust skull is characterized by a prominent sagittal crest and cheek bones (zygomatic arches), skull specializations which were essential for the manipulation of the massive jaw. Diet may have been similar for the two forms, but it has been suggested that the robust form was a more efficient herbivore.

Robust skulls have been found at nearby Swartkrans, another mile or so from Kromdraai, most notably the wellpreserved SK 48 skull. SK 48 apparently belonged to a female. It has been dated to 2 1/2 to 2 million years ago, the same approximate age as Kromdraai. More recent estimates place Swartkrans at 1.8 to 0.8 million years before present. There is obviously considerable uncertainty as to the absolute ages of the South African sites, and any dates must be regarded as conjectural.

Beginning in 1959, East Africa has yielded remains of hyperrobust australopithecines. These forms will be considered later. All of the South African robust forms, though, have been placed in the classification *Australopithecus robustus* , following Broom's species designation but not distinguishing the robust forms from the gracile generic designation. Pilbeam suggests that the larger body size and modifications in skull structure are explainable entirely within the context of the need for powerful muscles to operate the large jaws. Others have suggested that the gracile and robust forms are actually members of the same species, and that their differences in form reflect age and sexual differences, as well as geographical variation. It is not safe to assume at this time that all gracile forms are females and that all robust ones are males, however.

Australopithecus robustus became extinct approximately 1 million years ago, having survived relatively unchanged for as long as 2 million years. Its somewhat younger age than *A. africanus* , as well as the morphological differences it expresses, suggest that the robust australopithecines are specialized offshoots in the australopithecine line.

5. *Australopithecus boisei* (Zinjanthropus boisei—the nutcracker man)

Some of the key fossil discoveries of this century have been more a result of fortuity than of hard work, as was the case with Dart's and Broom's initial discoveries. Dart more than made up for it with his fouryear effort to separate the lower jaw of Taungs from its rock matrix, as did Broom with his 15 years of digging and writing. For Louis and Mary Leakey, pioneer hominid excavators of East Africa, the discovery of the famous Zinjanthropus skull was a culmination of nearly 30 years of laborious work. Louis Leakey began the careful exploration of Olduvai Gorge in the Serengeti Plains of Tanganyika (now Tanzania) in 1931. Through the 1930s, 1940s, and 1950s he and his wife Mary, who has been regarded as the more meticulous member of the team, discovered the remains of numerous extinct animals, and more importantly, stone tools of early human cultures—hand axes, choppers, and cleavers. The maker of these tools eluded the Leakeys for years, until they seemingly discovered a representative skull of his in 1959.

One midJuly day in 1959, while Louis nursed a case of the flu back at the base camp, Mary set out to examine an area of the Gorge. She noticed on that day a portion of skull protruding from the rocky ground. Summoning a revitalized Louis, the two spent the next 19 days carefully removing a nearly complete skull of a newly recognized hominid. Zinjanthropus boisei, the nutcracker man, was named after the ancient name for East Africa as a whole, "Zinj," and after Charles Boise, one of Leakey's financial backers. Some of the many important discoveries that followed demonstrated that Zinjanthropus was probably not the toolmaker of Olduvai; but the discovery of this Olduvai hominid, well promoted by Leakey, was one of the exciting paleontological events of the century.

Zinjanthropus lost its generic distinction when Phillip Tobias justified its reclassification as *Australopithecus boisei* in 1967. This hyperrobust australopithecine is characterized by a large sagittal crest and very prominent zygomatic arches. The canines and incisors are reduced in size, the chewing teeth are broad, and the forehead of Zinj is quite flat. The face is short and deep. It is the skull of a young male. Zinjanthropus has been accurately dated to 1.8 million years B.P. Unlike the sites of australopithecine hominids in South Africa, East African sites are very suitable for Potassium/Argon absolute dating. Olduvai provided a continuous geological and faunal history of 2 million years.

The cranial capacity of Leakey's *Australopithecus boisei* is estimated as somewhat larger than those of most other known australopithecines, 530 cc. Significant postcranial differences have so far not been recognized. As with *A. robustus* , the buttressing of the *A. boisei* skull is a specialized response to the increased size of the jaws and cheek teeth. This bipedal hominid probably fed on tough vegetable matter, such as nuts and roots.

In 1968, Richard Leakey, one of the famous couple's sons, and Meave Epps, who later became his wife, recovered a skull of *Australopithecus boisei* from the Koobi Fora region of Lake Turkana (formerly Lake Rudolph). The skull lacks teeth and the mandible, but is otherwise complete. Given the accession number KNMER 406 (previously FS158), the skull has a cranial capacity of less than 550 cc. The skull was originally dated at 2.6 million years B.P., but more recent analyses of the Koobi Fora sedimentary strata indicate that 2 million years ~ a more accurate estimate. As with the Zinj skull of Olduvai, this is a very robust skull.

6. *Homo habilis* ("able man" or "handy man")

The discovery in Kenya of skull KNMER 1470 by Bernard Ngeneo, a member of Richard Leakey's National Museum of Kenya expedition, is generally regarded as the find of this decade. Working in the Koobi Fora region of Lake Turkana (Lake Rudolph), Kenya, in 1972, Ngeneo noticed a number of bone fragments scattered over the surface of a slope. The pieces of bone were those of a hominid skull. Careful screening of 400 square meters of ground yielded several hundred fossilized fragments. As with many fossils recently exposed to the sun, wind, and rain, the brittle bones of 1470 had been damaged considerably. The process of fitting these pieces together into their proper orientations is best described as assembling a threedimensional jigsaw puzzle, when the puzzlesolver lacks some of the pieces. During the six weeks that followed recovery of the fragments, Meave Leakey, Alan Walker, and Bernard Wood were able to fit many of the pieces together, forming a very complete skull with a surprisingly large brain capacity, measured at 770775 cc. Tentative estimates of the age of Skull 1470 gave a range of 2.25 to 2.75 million years B.P. The younger age is presently favored.

This skull is characterized by a fairly high, steepsided cranial vault, slight brow ridge, and relatively thin cranial bones. The skull is now considered to be that of an early form of *Homo habilis* , the first hominid to be given the same generic designation as that of modern man. In this sense, *Homo habilis* can be regarded as the first true human.

Richard Leakey's description of the 1470 *Homo habilis* is not the first one for this species. Early *Homo* remains—mandibles, skull fragments, clavicles, tibiae and fibulae, hand and foot bones— were discovered at Tanzania's Olduvai Gorge beginning in 1960. The mandible found at Olduvai site F.L.K.N.N.I. was located by Richard's brother Jonathan. It serves as the type mandible for *Homo habilis* , that newly recognized species of *Homo* first described in the April 4, 1964 *Nature* article by the brothers' father, L.S.B. Leakey. (The name *Homo habilis* , "able man" or "handy man," was suggested to Leakey as an appropriate designation by Raymond Dart.) The Olduvai remains are given an age of 1.75 million years B.P.

Richard Leakey's 1470 skull is a very significant find for two reasons. It gave further confirmation to Louis Leakey's belief that early *Homo* lived contemporaneously with australopithecines, rather than being linearly descended and temporally separated from *Australopithecus,* Equally significant was the indication that the human ancestry can be traced back much earlier than had previously been believed. Skull 1470 added perhaps 500,000 years to the known age of *Homo* . (Subsequent discoveries at Olduvai, Lake Turkana, and elsewhere show that *Homo habilis* was fully adapted for upright walking and posture, and that he was a user of stone tools. Using a sample of 5 skulls found, *Homo* habilis had a cranial capacity of 600750 cc.)

7. *Australopithecus afarensis* ("Afar apeman")

Generally speaking, paleontologists can be referred to either as "splitters" or as "lumpers." The splitters tend to favor the use of new generic and specific names for their discoveries, when unique morphology is evidenced. When L.S.B. Leakey introduced the names "Zinjanthropus", "Kenyapithecus", and *Homo habilis* , he was emphasizing the uniqueness of those fossil forms. In contrast, the “lumpers” prefer simplifying the nomenclature by grouping similar fossil finds into the same genus, sometimes even the same species. They suggest that individual, sexual, geographical, and temporal variations must be considered in describing an evolving lineage, and that separate species designations be used only for those forms that are significantly different morphologically. Simons and Pilbeam exemplified this approach to taxonomy in the 1960s when they reassigned previously described Sivapithecus, Bramapithecus, and Kenyapithecus fossils to *Ramapithecus* . Splitters and lumpers agree that names assigned to fossils are important in that they suggest phylogenetic relationships.

It was with considerable interest, then, that students of hominid evolution received word late in 1978 of the new species designation, *Australopithecus afarensis* . Extensive examination of 3.8 to 2.9 million-yearold hominid remains from Laetoli in northern Tanzania and from Hadar in the Afar region of Ethiopia convinced Don Johanson, Tim White, and Y. Coppens that a new species of australopithecine had been found. (Initial statements had suggested that these fossils would be assigned to *Homo* .) There is not universal agreement that the Afar apeman merits new species classification, But this should not be surprising in a period when frequent fossil discoveries are forcing continual reexamination of the evidence. Scientists do agree that these earliest of welldocumented hominid remains will prove to be of great importance to the understanding of hominid evolution.

The combined analysis of fossils from Hadar and from the Laetolil Beds (in Laetoli) is an example of the recent preference among anthropologists for basing generalizations on collections of remains rather than on individual finds. Fossils recovered from surface examination and sieving of the two sites represent nearly one million years of evolutionary history, and they are believed to be of common populations—a single hominid lineage. Johanson is codirector, along with M. Taieb, of the International Afar Research Expedition, and the Frenchman Coppens is a member of this team. White, an anthropologist currently with the University of Michigan, has done field work with Mary Leakey’s team at Laetoli. The Hadar fossil material has been collected since 1973, with the most important find, the remains of an adult female hominid, “Lucy,” being made in November, 1974. Work at Laetoli has continued since 1974, with much of the material important to the description of this species being recovered during the 1974 and 1975 seasons. (Mary Leakey continues to direct work at Olduvai Gorge, as well).

Discovery of “Lucy” ranks as one of the great achievements in paleontological history, and her naming must rank with the classic examples of scientific humor. Early examination of the skeletal fragments of this three millionyearold hominid took place during a playing of the taped Beatles song, “Lucy in the Sky with Diamonds.” The name stuck. The “Lucy” skeleton is 40% complete. Cranial remains are limited, but a good mandible was found. The postcranial skeleton, usually poorly represented in the fossil record, is of primary importance. It indicates that this 3.5 to 4.0 foot tall hominid was welladapted for bipedal locomotion. Fossil hand bones from a nearby Hadar locality bear strong resemblance to the modern human hand, in their apparent manipulative ability. “Lucy”, who received the catalog designation A.F. (Afar Locality) 2881, is estimated to have been in her twenties when she died. PotassiumArgon dating techniques suggest that she and the dozen or so other individuals whose remains were recovered at Hadar lived 3.3 to 2.6 million years B.P. Five to seven of the hominids found in association with each other may have comprised a family unit.

Hominid remains from the Laetolil Beds are somewhat earlier than those from Hadar, being 3.83.6 million years old. The mandible L.H. (Laetoli Hominid) 4 is the type mandible for the species *Australopithecus afarensis* . This mandible, as with the others recovered at both sites, is relatively light, with a Vshaped dental arcade. The appearance of the jaw, as well as the robustness of the postcranial skeleton are examples of the retention of apelike characteristics in *Australopithecus afarensis* .

A high Level of sexual dimorphism characterizes these fossils. This interpretation is preferred to the possibility that these are not male and female variances, but rather two different species of Hominids. *Australopithecus afarensis* has been proposed as that form which subsequently diverged into australopithecine and human lineages. The discovery at Laetoli, East Africa of 316 millionyearold fossil footprints by members of Mary Leakey's fossil hunting team confirms very early erect walking. The footprints, left by Afar apemen, indicate that the pelvic girdle, the leg bones, and the angle of the foremen magnum for this hominid were essentially those of modern man. Increase in brain size, however, is a relatively recent development, which experienced acceleration approximately one million years ago.

In discussing some of the more salient aspects of current evolutionary thought, an effort has been made to avoid considering earlier forms of hominids as incomplete or imperfect humans. It is a mistake to regard earlier forms only in relation to modern man, or to suggest that the evolutionary process of the past 15 million years has been one of direction toward producing today's man. Earlier hominids had their own unique qualities, and these species enjoyed long periods of successful existence. *Homo sapiens* is a species that has been present on earth for approximately 200,000 years, as compared with 1 million years for Homo erectus or for *Australopithecus robustus* . Another aspect of our uniqueness is that we happen to be the sole surviving representatives of a family that was formerly diverse. Our longrange success as a species and the evolutionary trends that we continue to express are matters which remain to be seen.

V. Current Views of Hominid Evolution

Through the scientific efforts of the past several hundred years, we now know that the earth is an ancient planet, that it has undergone extensive physical change, and that it continues to evolve in appearance. We also know that all forms of life undergo changes in appearance and functional ability over the course of generations. Fossilized remains of earlier forms of life indicate that different species evolve at different rates. The socalled "living fossils," such as the Ginkgo, the cycads, the dragonfly, the shark, and the coelocanth, have remained largely unchanged for millions of years. They contrast with such organisms as the horse and the elephant, whose evolutionary histories of 40+ million years show major changes. Horselike forms, for example, underwent changes from foot high, fourtoed mammals to the fiveto six-foothigh, onetoed forms of today.

Species are mutable. It is also true that many earlier forms of life are extinct—in excess of 90% of all life forms ever to have inhabited the earth. Some of these forms have become "extinct" in the sense that they have been transformed through genetic mutation or hybridization into new and different forms. Many types of life have been evolutionary deadends, however—evolutionary experiments which, though they may have been welladapted for long periods of time, did not enjoy the luxury of descent to the present. (It should be realized that despite use of the term "evolutionary deadend," with its unfavorable connotation, no suggestion of inferiority or of reduced significance for lineages that have died out is intended. The one constant in the biological history of the earth is change.)

Despite protestations to the contrary, man too has experienced change in form and function over a long period of time. We are animals, more specifically mammals, whose present exalted state represents a unique response of reproducible genetic material to environmental forces. That unique feature about us which is most prominent and most deserving of (our own) awe is our large and complex brain, an organ which is capable of the most sophisticated of functions. Green algae, grasshoppers, and gibbons have their own unique features. Such a realization in no way diminishes appreciation for the marvels of the human species; it merely heightens appreciation.

A primate, man bears many obvious similarities to the great apes, monkeys and prosimians, the other types of primates. Chemical studies of blood proteins have shown that the great apes—chimpanzees and gorillas in particular—are more closely allied in genetic makeup to man than they are to the other primates. The implication is that they are more closely related to us phylogenetically. The developing discipline of molecular evolution suggests a divergence of hominids away from pongids as recently as five million years ago. The earliest known anthropoids are 40 million year old (Eocene) forms, found in 1978 in Burma by Russell Ciochon and Donald Savage. *Amphipithecus* and *Pondaungia* are believed to be at or near the point of divergence of apes and monkeys. A possible 40millionyear separation in development for apes and monkeys is to be compared with a possible 5 million year separation of the apes and hominids.

As has been stated, the early hominids, organisms directly or closely related to our own species and including *Homo* , have been recovered from once tropical savanna and open grassland regions of Africa, Asia, and Europe. Most individual organisms of past eons did not leave fossilized evidence of their existence; rather, they underwent total decomposition, the result of weathering, scavenging, decaying. This is particularly true in tropical areas of the world, and it is particularly true of the hominids. Hominid remains are fragmentary and incomplete. Despite the great increase in recent years of the fossil evidence for hominid evolution, when one considers the long time during which hominids have evolved, the large numbers of generations of individuals that span the past 5 to 10 million years, and the extreme unlikelihood that the complete fossil record exists or will be recovered, it is safe to say that direct linear descent of man from his precursors will never be established. What we do have available to us is best described as evidence of occasional moments in hominid evolutionary history, a fragmented, threedimensional jigsaw puzzle with a fourth, temporal dimension added.

We need not be committed to total disappointment in trying to satisfy our curiosity about our origins. Examination of the fossil evidence at hand can reveal much about lines of development and evolutionary trends undergone over time by members of the Family Hominidae. Major trends in hominid evolution include refinement of bipedal locomotion (probably the most significant evolutionary development), increase in brain size, and refinement of stereoscopic vision with a concurrent reduction in the importance of the sense of smell. Shortening and flattening of the face is related to the abovementioned changes.

In the 120 years since Charles Darwin delineated his theories of evolution in *On the Origin of Species* , all aspects of Darwinian evolution have come under attack. Darwin was familiar with a number of extinct fossil forms, having collected a variety of fossil remains while serving as a naturalist on board the H.M.S. Beagle in the 1830s. The fossil evidence for human evolution was sparse in the second half of the nineteenth century, however, and it was of little help to Darwin in his formulation of theories of man's descent. The principles of Mendelian genetics have served to reinforce Darwinian theory, while recent genetic studies using techniques of DNA recombination, hybridization, and gene sequencing have revealed a more complex process of protein synthesis, and raised new questions about the importance of natural selection to the evolutionary process. Nevertheless, Darwin's basic formulations are still generally regarded as valid.

Species adaptation through natural selection, according to Darwin, is the principal vehicle for evolution. Darwin recognized that all living things are theoretically capable of rapid and enormous increase in numbers—geometric increase. Most populations of organisms, however, experience arithmetric increase, or tend to remain fairly constant in numbers over time. Darwin concluded that forms of life seldom if ever enjoy optimum conditions for growth and reproduction, that they are all faced with a struggle for survival. At the same time, species are made up of collections of individuals exhibiting a variety of morphological and functional characteristics. Adaptations can be of greater or lesser advantage to individual organisms. Ultimately, some organisms are more successfully adapted to their surroundings than others. (These adaptations, it should be emphasized, arise randomly and passively.) Environments eventually change, and new advantages may be bestowed on previously insignificant adaptations. Over a period of time, those individuals which are best adapted will tend to survive and pass on their traits through reproduction.

Development of new species is the fundamental process of evolution. This process, called speciation, is believed to occur in one of the following fashions. A population of individuals of the same species inhabits a distinct, perhaps widespread, geographical area. Individuals at one extremity of the population range may be somewhat different from individuals at the other extremity of the range. There is a continuity of characteristics across the range, however, and although individuals at one extreme may not come into contact with or mate with individuals at the other extreme, they remain capable of successful mating and production of viable, fertile young. They are also reproductively isolated from other species. These are the criteria for determining if two organisms are of the same species.

It is at this point that theories differ as to how speciation takes place. One school of thought says that genetic drift—the gradual accumulation of neutral, nonadaptive gene mutations in stable populationsis the principal driving force of evolution. Darwinian evolutionists, on the other hand, maintain that natural selection by survival of favorable adaptations is the prime mover. They disagree among themselves as to the method of speciation. The theory of sympatry holds that two species can develop from one parental stock through natural selection, while individuals continue to live side by side. Selection pressures result in a divergence away from common characteristics, until such time as the two groups cannot interbreed.

Allopatry depends upon geographical splitting for speciation to occur. At some point, which may be relatively abrupt, a local group at one of the geographical fringes becomes isolated from the rest of the population by geographical barriers. The genetic diversification which follows from this formation of two separate breeding populations becomes sufficiently great that subsequent reintroduction of the two branches into the same geographical range does not result in successful interbreeding. Two separate species now exist, where formerly there was one. Both species may persist, or only one may survive to undergo further speciation. In geological time, the process of speciation may be a very rapid one, involving no more than hundreds or thousands of years. This view of a stop andgo form of evolution is at variance with the more traditional view of evolution as a long, gradual process. It is easy to imagine significant changes occurring where selection pressures are greater and species survival is more tenuous. Characteristics always appearing in a population through variation and mutation, if advantageous to the individuals' survival, would have greater likelihood for retention in the fringe group.

The case for evolution by chromosomal change has been strengthened recently by studies on two closely related lesser apes, the gibbon and the siamang. These two apes are believed to have diverged from a common ancestral stock fifteen million years ago. They are sympatric, occupying the same tropical forests of Southeast Asia. Classified in different genera, gibbons and siamangs are not known to interbreed in the wild. In August of 1975 at the Grant Park Zoo in Atlanta, Georgia, a hybrid offspring was formed from the unexpected mating of a male gibbon and a female siamang. A second hybrid was born the following year, but it died of infection at an early age. The firstborn hybrid, now four years old, is being called a siabon. There has been much recent publicity about this firstknown hybrid between two species of apes.

The evolutionary significance of the gibbon and the siamang is not that they are capable of hybridizing. A number of other hybrid animals are known, including offspring from lions and tigers and from horses and donkeys. Their significance is that their genetic material produces very similar structural proteins, while the number of chromosomes for each species and the gene sequences on their chromosomes differ greatly. Siamangs have a diploid set of 50 chromosomes and gibbons have a full complement of 44 chromosomes. Siamang chromosomes are almost completely nonhomologous with gibbon chromosomes.

Speciation of the gibbon and the siamang from their ancestral stock appears to be the result of chromosomal changes and consequent reproductive isolation. (The siabon hybrid, as with most other hybrids, is believed to be infertile.) This speciation may well have originated rapidly and nonadaptively. If such is the case, then evolution does not merely occur by gradual accumulation of genepoint mutations.

Whether speciation takes place as a result of geographical or genetic barriers, adaptation and natural selection or nonadaptive chromosomal change, it is a process that takes place repeatedly. The traditional view of evolution is one of a linear progression of ancestors and descendants, extending from the distant past to the present. The image of a ladder is often used to represent this progression, and the ladder seldom has side rungs. Harvard biologist Stephen Jay Gould prefers the image of a bush with numerous branching. This is a far more complicated picture of evolution, and it suggests that we can expect to find many more types of hominids in the unfolding fossil record species which very likely are not directly on the human lineage. Gould notes that archaic parental stocks may persist long after giving rise to newer species, and this is reflected in the fossil record.

Whereas scientists once constructed these ladders of descent to explain the evolution of hominid ‘lines’, there is an increasing tendency to generalize interpretations about the fossil record. David Pilbeam suggests that the more objective approach is to consider dryopithecines, ramapithecines, pongids, and hominids as groups. Modern pongids, then, are descended from the dryopithecine group. The genus *Homo* emerged from a portion of the australopithecine group, they evolving from ramapithecines or perhaps even from dryopithecines. *Ramapithecus* may or may not be on the human lineage. It was one of the first forms to exploit open grassland habitats, but it may have been an early, unsuccessful experiment.

We can talk with somewhat more assurance about the more recent evolutionary history of hominids. Johanson and White propose that the Afar apeman, *Australopithecus afarensis* , was an ancestor both to the later forms of australopithecines and to *Homo* , They feel that divergence occurred between 3.0 and 2.5 million years ago. One branch led to *Australopithecus africanus* and then to the more specialized *A. robustus* and the variant *A. boisei* . The other major branch led to *Homo habilis* , the earliest member of the genus *Homo* . Portions of the *H. habilis* population gave rise to *Homo erectus* , and part of the *H. erectus* population led to development of *Homo sapiens* . Modern man emerged as recently as 40,000 years ago.

Examination of the trends in evolution indicate that not all organ systems have evolved at the same rates. The concept that different features of an organism evolve at different rates is known as mosaic evolution. Efficient bipedal movement is a trait that appeared very early, and it is probably the single most important development in the emergence of man.

VI. Conclusion

In the previous sections of this narrative, the attempt has been made to illustrate some of the changes in thinking that have occurred in interpreting the fossil record and explaining the mechanisms of evolution. Historical considerations are useful in pointing out that both the physical and the biological sciences are in a continual state of flux. The sciences attempt to describe natural events in an orderly fashion. The history of scientific thought involves a succession of models—called paradigms by Thomas S. Kuhn—for describing as accurately as possible those natural events. The paradigms are essentially the consensus opinions in the various disciplines of science, and they may be regarded as forms of dogma. Scientific research in effect involves an attempt to fit acquired data to the existing paradigms. A paradigm provides a foundation on which continued scientific work builds.

Darwinian evolution, for example, is a current form of scientific dogma, as is the "holy trinity" of DNA, RNA, and Protein in the areas of genetics and protein synthesis. Kuhn calls this reliance on paradigms "normal science." During those occasional moments in the history of a science when anomalies surface which will not fit into the existing paradigm, a crisis in science results. When a new paradigm which better explains observable phenomena is formulated, what Kuhn calls a scientific revolution takes place. The old paradigm is discarded and the new one becomes dogma.

The above statements are a poor attempt at summarizing Kuhn's views of the scientific process. They do indicate that science is not merely a gradual accumulation of knowledge. It is, however, correct to say that science is an attempt to describe "truth" and "reality" in more accurate terms. I prefer terms such as "truth" and "reality" to "fact" in talking about science, for we know that today's facts are tomorrow's myths. Good scientists may be staunch supporters of their paradigms, but they keep in the backs of their minds the awareness that some of what they avow will ultimately be discarded. The two quotations that follow, the first by Karl Pearson and the second by W.E. LeGros Clark, provide clear perspective for an understanding of the workings of science.

> Science consists not in absolute knowledge, but in the statement of the probable on the basis of our present—invariably limitedacquaintance with facts.1

> [Working hypotheses] form the basis of research projects. In due course, new evidence usually requires the modification, if not the abandonment, of such hypotheses. This, however, is how the scientific method works. It amounts to a stepbystep and ever closer approximation to the truth, and implies that all hypotheses, unless they take a very general form . . . are necessarily going to be superseded as science progresses.2

This concept is perhaps the most basic one that a science teacher can hose to communicate to his students.

VII. Unit Outline and Sample Lesson Plans

Unit Outline

I. Introduction.

	Lesson 1:	Introduction to the study of hominid (23 days) evolution—the diversity of life (variation; plant and animal adaptations; Evolution—the unifying theory of biology (a review, making use of slides and photographs).
II.	The Magnitude of Geological Time.	
	Lesson 2:	Preparation of a Cosmic Calendar.
	(2 days)	
	Lesson 3:	Generation Time.
	(1 day)	
III.	Methods for Studying Hominid Evolution.	
	Lesson 4:	Identification of Bone Fragments
(	12 days)	The Cat and the Dog.
	Lesson 5:	Slides: Yale Peabody Museum of Natural
	(1 day)	History—A Fossil Dig in New Jersey.
	Lesson 6:	Language used in the study of hominid
	(12 days)	evolution. (Slides: Hominid and Pongid Fossils of the Yale Peabody Museum Collection.)
IV.	The Fossil Record—Key Discoveries of this Century.	
	Lesson 7:	Slides: Hominid Evolution—The Fossil
	(1 day)	Evidence (pongids, dryopithecines, ramapithecines).
	Lesson 8:	Readings—Hominid Evolution
	(1 day)	
	Lesson 9:	Slides: Hominid Evolution—The Fossil
	(1 day)	Evidence (hominids).
	Lesson 10:	Readings: Hominid Evolution.
	(1 day)	Writing Assignment.
	Lesson 11:	Preparing Plaster Casts.
	(2 days)	
	Lesson 12:	MapMaking—Sites of Major Hominid
	(1 day)	Fossil Finds (Africa, Asia, Europe).
V.	Current Views on Hominid Evolution.	
	Lesson 13:	Relating Structure and Function
	(1 day)	Bipedal Locomotion.
	Lesson 14:	Preparation of a Phylogenetic Bush.
	(12 days)	
VI.	Conclusion.	
	Lesson 15	Review and Evaluation of Unit.
	(1 day)	

Hominid Evolution ***: Identification of Bone Fragments—The Cat and the Dog***

Instructions:	Scientists usually do not find complete fossils whenthey search likely sites. A broken skull, a jawbone, or
(work with	just a piece of tooth may be all that is left of a
your lab	oncecomplete skeleton. This laboratory activity is
Partner)	designed so that you can learn something about how scientists identify pieces of bone fossils. *Read the information below and work with the bones that you have been given. Answer all questions on this paper* .
Materials:	One complete, unassembled skeleton (a cat or a dog.) Bone fragments from the same type of animal. A diagram of the cat or the dog skeleton.
Procedure:	1. Spread out the bones from the complete animal skeleton, dividing them into groups of similar bones. For example, the rib bones all look like each other, and they go into one pile. Vertebrae go together, as do long leg bones. Any odd bones left over can be put into one pile.
	2. *Which bones from the skeleton are the largest bones* ? (Refer to the diagram of the cat/dog skeleton if you do not recognize the bones by name.) *Which bones are probably the hardest bones of the skeleton? Which bones are the thinnest and the most likely to be broken in time?*
	3. Examine the bone fragments that have been given to you separately. These bones are the remains of fairly large, hard bones of either a cat or a dog. Do any of the bone fragments match bones in your collection *?* Which ones? *(Name them).* How certain are you that you have correctly identified these fragments *? List* two or three clues that you used in identifying each bone fragment *.*

4. Take the bone fragments that do not match your collection of skeletal bones and match them to bones in someone else's collection. *Name these bones, using the new skeletal diagram.* In what ways are these bones different from *the ones found in your collection? How certain are you that you have correctly identified these fragments?*

Hominid Evolution: Slides— *The Fossil Evidence*

(pongids, drypoithecines, and ramapithecines)

Instructions: Today you will be seeing a series of slides of living apes, as well as fossils of some animals that are no longer found on earth. Study the slides, follow the class discussion about these photographs, and answer each of the following questions.

slide 1:	The gibbon (*Hylobates*): This ape spends nearly its entire life in the trees of tropical forests. It moves by a method called *brachiation.* Briefly, describe what brachiation is.
slide 2:	The orangutan (*Pongo pygmaeus*): Orangutans are quite rare and are found in the forests of Borneo and Sumatra. They are also arboreal. Define the term arboreal.
slide 3:	The gorilla (*Gorilla gorilla)* : Gibbons, orangutans, and gorillas are three of the apes. Name the fourth type of ape.
slide 4:	Chart—Primate Characteristics: This chart shows information about the different types of primates, the tarsiers, femurs, New World monkeys, Old World monkeys, apes and man. List at least three ways that apes and humans are different from the other primates.
slide 5:	Olduvai Gorge, Tanzania, East Africa (aerial view): This is one of the famous sites where a number of fossils of extinct hominids have been found. Louis and Mary Leakey are the husbandandwife team that worked in this region of East Africa for more than 40 years.
slide 6:	Turkana, northern Kenya: This picture shows another well known site for finding fossil hominids. What is a hominid?
slide 7:	Turkana, northern Kenya: In this photograph, Richard Leakey, son of the famous Louis and Mary Leakey, is examining a fossil with Bernard Ngeneo, a member of the fossilhunting team.

slide 8: Comparison: *Aegyptopithecus* , *Pliopithecus. Hylobates* : List three ways that the gibbon skull on the right is similar to the 28million and 20millionyearold fossil skulls. Refer to the next two slides.

slide 9: Comparison: *Aegyptopithecus* , *Pliopithecus* , *Hylobates* .

slide 10: Comparison: *Aegyptopithecus* , *Pliopithecus* , *Hylobates* .

slide 11: *Limnopithecus* : This fossil jaw with teeth is all that remains of this ape that lived 23 to 14 million years ago. List those bones of the skeleton which you think are the hardest.

slide 12: *Dryopithecus africanus* : Mary Leakey found this skull in Kenya in 1948. It is the bestpreserved skull ever found of an early ape. This primate lived perhaps 16 million years ago. Does it remind you of an ape or of a human? Why?

slide 13: *Dryopithecus nyanzae* and *Dryopithecus fontani* : These jawbones belonged to two similar apes.

slide 14: Comparison: *Gorilla* (left) and *Dryopithecus* (right): Some scientists believe that apes like *Dryopithecus* were the early ancestors of today's gorilla or chimpanzee. What similarities do you see between these upper jaws?

slide 15: *Oreopithecus* : This 14millionyearold ape had long arms and probably moved by brachiation.

slide 16: *Oreopithecus* reconstruction: By studying the bones of extinct animals and knowing something about where the animals lived, an artist can try to reconstruct what the animals looked like when they were alive.

slide 17: *Ramapithecus* : This primate, which lived over a period of from 12 to 8 million years ago, has left fossils in a number of areas in Africa, Europe, and Asia. Only jaws, teeth, and cheek teeth have been found, however. Some scientists have felt that it was the first hominid (ancestor of man) and that it walked upright. Recent finds have suggested that it is more apelike. Name several ways in which apes are different from humans.

Hominid Evolution* : Slides— *The Fossil Evidence

(the hominids)

Instructions : |The slides which you saw earlier were photographs of apes alive today and apes that lived between 8 and 30 million years ago. Today you will see photographs of extinct primates that are considered humanlike. As we discuss each of the slides, write answers for the following questions.

slide 1: *Australopithecus africanus* : the Taungs baby

This skull was found in 1924 in a quarry in Taungs, South Africa. It was given to Raymond Dart, who removed it from the surrounding rock and described it. The primate that owned the skull was about 5 or 6 years old when it died. Its brain was about 1/3 the size of ours. Dart felt that it was very humanlike in appearance.

slide 2: *Australopithecus africanus* : This skull of a femme in her twenties was found in Sterkfontein, South Africa in a quarry, in 1936. It was given to the scientist Robert Broom. The skull demonstrated that the Taungs baby skull was not that of a freak, but rather of a different type of life. Both skulls are 2 to 3 million years old. In what ways do they look human?

slide 3: *Australopithecus africanus* : This skull is the one you saw in the last photograph. It has been put together with a jaw found nearby, but probably belonging to another individual.

slide 4: *Australopithecus robustus* : In 1938 Robert Broom was given a skull found in Kromdraai (KromDry) South Africa by a young schoolboy. This skull was larger than the *A. africanus* skulls, and had a very large lower jaw. The skull and jaw in this photograph are similar to this new type of skull. What do you notice about the teeth in the lower jaw?

slide 5: *Australopithecus robustus* : If you were to go to the Transvaal Museum in South Africa, you would see this skull. Notice the ridge of bone on the top of the head. Muscles attached to this ridge (the sagittal crest). Why did this hominid need enormous muscles attached to the top of its head?

slide 6: *Australopithecus robustus* : The skull shown here and in the next photograph was found in Swartkrans, South Africa, very near Sterkfontein and Kromdraai. Apes have long, deep faces. Humans have short, vertical faces. What kind of face does *A. robustus* have?

slide 7: *Australopithecus robustus*

slide 8: Australopithecus boisei *: Meave Epps and Richard Leakey found this skull at Koobi Fora, Lake Turkana in 1969. It is 1.6 to 1.3 million years old. This hominid was bigger than* A. africanus *and* A. robustus *and may have weighed 100 to 150 pounds. Notice the crest on top of the skull. The first skull of this type was found at Olduvai Gorge by Mary Leakey. It was then called "Zinjanthropus".*

slide 9: *Australopithecus* reconstruction: An artist who is familiar with muscles and bones has begun reconstructing this *Australopithecus* as it may have looked.

slide 10: *Australopithecus boisei* reconstruction: *What is your first reaction when you see this artist's drawing?*

slide 11: Australopithecus boisei *jaw:* Are these teeth U shaped (teeth parallel on either side), Vshaped, or parabolic?

slide 12: Comparison: Australopithecus africanus *and* Australopithecus robustus *: You have seen both these skulls before.* Which one is A. africanus and which is A. robustus?

slide 13: Comparison: Australopithecus africanus *and* Pongo *(the orangutan):* What is the most obvious thing about the teeth of this male orangutan *?*

slide 14: Comparison: *A. africanus* and *Homo sapiens* (man): That is you on the right! *Compare your brain size with the brain for Australopithecus* .

slide 15: *Homo habilis* : This is the famous 1470 skull found by Richard Leakey's team in Kenya. It is about 2.50 million years old.

slide 16: AfarHadar Region of Ethiopia: Fossil hominids have been found here.

slide 17: Don Johanson with "Lucy": *What is the new name given to these 3millionyearold bones?*

slide 18: Homo erectus (male): Where were this and the skull in the next picture found?

slide 19: Homo erectus (female)

slide 20: *Homo sapiens* : We are members of the species Homo sapiens.

This H. sapiens skull is 150,000 to 200,000 years old. Doesit look human?

slide 21: Cartoon, Mr. Bergh to the Rescue: Why is the gorilla upset?

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Notes

1. Karl Pearson, quoted in *The Fossil Evidence for Human Evolution* (W.E. LeGros Clark), Third Edition, The University of Chicago Press, Chicago and London (1978), p. 204.

2. Clark, W.E. LeGros, *The Fossil Evidence for Human Evolution: An Introduction to the Study of Paleoanthropology* . Third Edition.

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Student Reading List

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Johanson, Don C., "The Quest for Early Man in Ethiopia," *The Explorer* , *16* (4), 4 (Winter 1974). A readable account by an anthropologist of life at the fossil hunting camp and the significance of fossil finds.

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Classroom Materials

Slide Set I—Hominid Evolution: The Fossil Evidence (pongids, dryopithecines, ramapithecines, hominids)

Slide Set II—Hominid and Pongid Fossils of the Yale Peabody Museum Collection

Slide Set III—Yale Peabody Museum of Natural History: A Fossil Dig in New Jersey

Instructions and Materials for preparing plaster casts

Sets of unassembled cat and dog skeletons

Also available for the teacher: reprints of all articles referred to in this unit; a series of recent newspaper articles on various aspects of hominid evolution.