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Ramapithecines and Human Origins

The Ramapithecinae, an extinct subfamily of anthropoid primates, are regarded by some workers as the oldest and most primitive members of the Hominidae, the family of man. Species of this group are similar in size to living apes and may have been broadly similar to them in habits. A marked characteristic of ramapithecines which unifies them as a group, and suggests an ancestral relationship to *Australopithecus*, is the extremely thick enamel on their cheek teeth, which appears to have been associated with an ability to consume extremely hard forest nuts. The vernacular term "thick-enameled apes" may justifiably be applied to the group (Fig. 1).

First appearing in the Miocene Epoch about 15 million years (m.y.) ago in East Africa and Turkey, ramapithecines achieved their greatest distribution about 10-8 m.y. ago when they had spread into central Europe, Greece, Pakistan, India, and China and were represented by no fewer than seven species. *Gigantopithecus*, a giant ape bigger than the mountain gorilla, from India, Pakistan, and China survived as a contemporary of early *Homo* until perhaps 1 m.y. ago. Other, less specialized branches of ramapithecines gave rise to *Australopithecus*, the earliest bipedal hominid, the oldest known occurrence of which is about 5.5 m.y. ago.

Among ramapithecines two genera are generally recognized, *Sivapithecus* and

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Fig. 1. Hypothetical reconstruction of middle Miocene *Sivapithecus* as it would have appeared in life. (Drawing by Donna Gregory)

Gigantopithecus, each containing several species. Discoveries of many fossils over the past 10 years demonstrate the great similarities of known parts (mostly jaws and teeth) among all ramapithecines, similarities which obviate the need to further subdivide *Sivapithecus* as some authorities do by continuing to recognize *Ramapithecus* and *Ouranopithecus*. These finds also show that although ramapithecines should be regarded as hominids because of their unique genealogical affinity with humans, they are much more primitive, or apelike, than had been recognized hitherto. This article gives a historical outline of the principal discoveries and a summary of the reasons for thinking ramapithecines are hominids. It also provides an analysis of the fossils for clues which would shed light on their adaptations.

HISTORY OF STUDY

An account of a ramapithecine fossil was first published in 1837, describing an upper canine tooth obtained from the Siwalik Hills in North India. This and other fossils from the Siwaliks range in age from 13 to 8 m.y. The authors of the report felt that this tooth, now lost, was that of an orangutan. In 1879 the British naturalist R. Lydekker described a ramapithecine palate with most of the teeth on one side. He called this specimen *Paleopithecus sivalensis*, and this name would continue to have been the standard attached to the group as a whole, were it not that *Paleopithecus* had already been applied in a German publication to fossil footprints of dinosaurs which were mistakenly thought to be those of an extinct "colossal age." In 1910 Guy Pilgrim named *Sivapithecus indicus* and in later papers advanced in great detail the idea that this animal was intimately attached to the human lineage, an idea which had been considered briefly by Lydekker in 1879. Pilgrim also described several other genera and species of fossil apes and considered them to be related to various living apes. It is now known that all the ape specimens he described are parts of several closely related species which take the name *Sivapithecus* and *Gigantopithecus*. Since those early finds, India and Pakistan have continued to yield many ramapithecine fossils. A joint Yale University-Geological Survey of Pakistan expedition to the Potwar Plateau area, under way since 1973, continues to recover important new specimens, including recently a part of a face of *Sivapithecus* and several fragmentary limb bones, the first known which definitely belong to ramapithecines.

European finds. The jaw of a large European ape was found in 1856 near the village of Saint-Gaudens, France, from a site where clay was being mined to make bricks. Edouard Lartet described this as *Dryopithecus fontani*. Later, isolated teeth recovered from deposits of the Vienna Basin in Germany were thought to belong to *Dryopithecus*, but several of these may belong to *Sivapithecus*. These and other European fossil apes are between 15 and 10 m.y. old. In recent years the scene of European discovery has shifted to Greece, the Balkans, and Turkey. Of particular importance are the finds of more than a dozen jaw fragments in one stratigraphic level in Macedonian Greece by a joint Greek and French expedition (Fig. 2). In 1980 Turkish and British paleontologists described a new facial fragment of *Sivapithecus* from near Ankara, Turkey (Fig. 3). Additionally, M. Kretzoi, a Hungarian paleontologist, has made many discoveries of *Sivapithecus* from coal layers near Budapest.

African finds. Between 1932 and 1935 L. S. B. Leakey's East African archeological expeditions made collections of ape fossils, among which was an upper jaw fragment with three teeth from Kenya. It was not until 1950, however, that the English anatomist Wilfred E. Le Gros Clark with Leakey

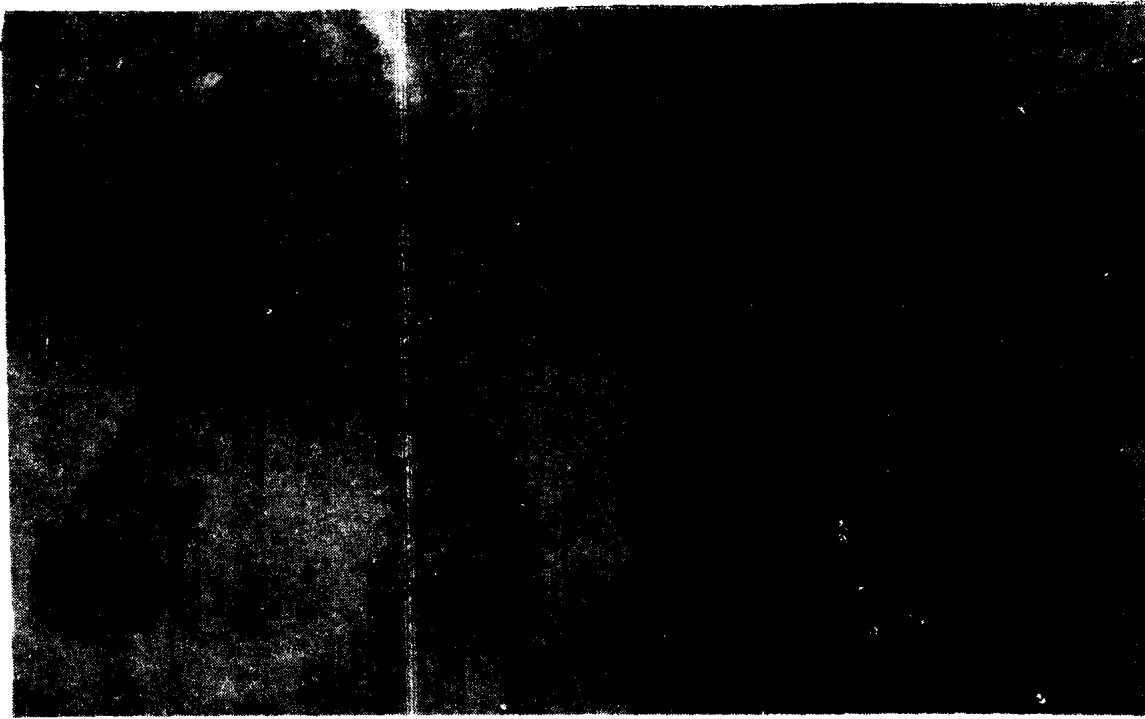


Fig. 2. Specimens of ramapithecine (a) lower jaw and (b) palate. (Courtesy of L. de Bonis)

recognized that this specimen was that of *Sivapithecus*, marking the first recognition of a ramapithecine from Africa. Since then, a handful of new specimens of ramapithecines have been discovered in Kenya at Fort Ternan and near Maboko Island (in Lake Victoria), most of which range in age between 15 and 13 m.y.

Chinese finds. Perhaps the most exciting finds of the last decade have been made in China. Until recently, Chinese *Sivapithecus* was known from a few isolated teeth described in the 1950s. However, expeditions starting in 1975 carried out by the Academia Sinica and the Yunnan Provincial Museum have recovered hundreds of new specimens aged roughly between 10 and 8 m.y. from coal fields close to Lufeng in Yunnan Province. Several beautifully preserved lower jaws have been described so far; pictures and accounts in the Chinese foreign language press indicate that as many as six crushed skulls (Fig. 4) are now known. As this material becomes better documented scientifically, it may revolutionize the understanding of ramapithecine adaptations and relationships.

SOME APE-HUMAN CONTRAST:

To set the stage for an assessment of details of ramapithecine anatomy, the anatomy and behavior of living great apes must first be considered in contrast with that of the earliest prehuman, *Australopithecus*, from Africa. The reason is that it has long been assumed, and rightly, that humans passed through a stage in their evolution in which they resembled living apes in many respects. Therefore,

knowledge about living apes gives insight about early stages of human evolution. Furthermore, the spectrum of ape-human contrasts can be used as a heuristic device to visualize the closeness of approach of ramapithecines to the human condition.

The great apes are man's closest living relations; smaller "lesser apes," the gibbons, are more distantly related. There are four species of great apes (Table 1 and Fig. 5): the common chimpanzee and bonobo chimpanzee (*Pan troglodytes* and *P. paniscus*, respectively) and the gorilla (*Gorilla gorilla*)

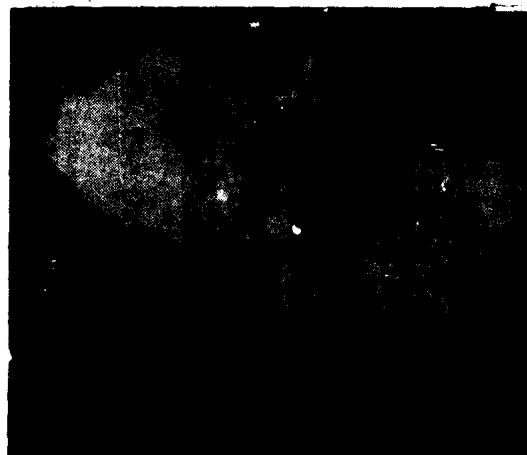


Fig. 3. Front view of a snout and face of *Sivapithecus* from the late Miocene of Turkey. Note the large size of canine teeth. The bottom of the right orbit is preserved at the top. (Courtesy of P. Andrews)

4 Ramapithecines and human origins

Table 1. Taxonomic groups of apes, humans, and prehumans

Family	Living forms	Extinct forms
Pongidae (all great apes)	<i>Pongo</i> (orangutan of Borneo and Sumatra) <i>Pan</i> (chimpanzee and bonobo of Africa) <i>Gorilla</i> (gorilla of Africa)	<i>Proconsul</i> (22–14 m.y.; several species from Africa and Saudi Arabia) <i>Dryopithecus</i> (15–10 m.y.; several species from Europe, southern Russia, and ?Africa)
Hominidae (humans and prehumans)	<i>Homo</i> (human beings)	<i>Australopithecus</i> (5.5–1.5 m.y.; from Africa) <i>Sivapithecus</i> (includes <i>Ouranopithecus</i> and <i>Ramapithecus</i> ; 15–8 m.y.; from Africa and Eurasia) <i>Gigantopithecus</i> (9–?1 m.y.; from Asia)

live in Africa; and the orangutan (*Pongo pygmaeus*) lives in Borneo and Sumatra. Orangutans formerly inhabited parts of Southeast Asia, China, and Java but are now extinct there. Except for some fossil orangutan teeth of recent age, there is no fossil record of any of these living species.

Details of the anatomy and biochemistry show that African apes (gorilla and chimpanzee) are more closely allied to humans than is the orangutan. Some biochemists would go further and claim, based on their molecular studies, to place rather precise times for the branching of these lineages from one another. However, the validity of their approach has been challenged for a variety of sound reasons. It appears that study of molecular structure provides useful information for assessing relationships, as do details of the gross and microscopic anatomy of animals, but none can precisely deter-

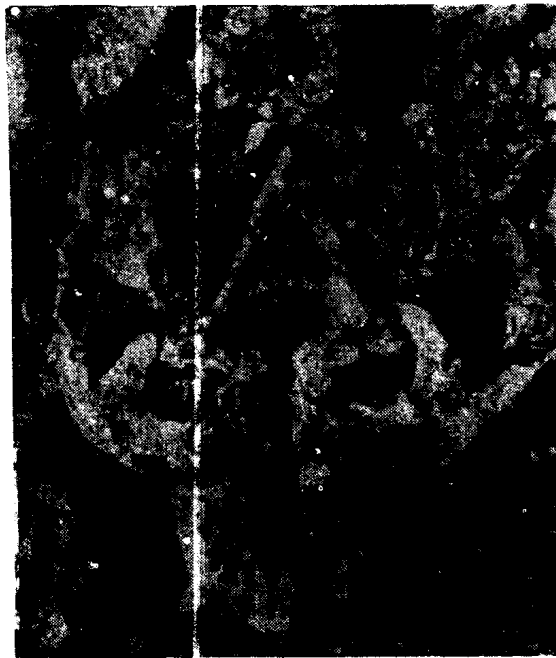


Fig. 4. Badly crushed skull of *Sivapithecus* from the late Miocene of Lufeng, China. Front teeth are at the bottom. Orbits, nasal opening, and flaring, jug-handlelike zygomatic arches are also visible.

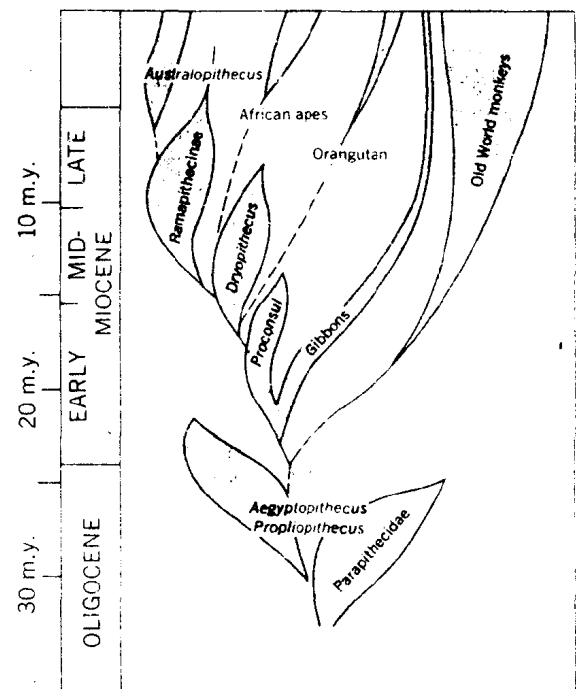


Fig. 5. Tentative phylogeny of monkeys and apes of Africa, Europe, and Asia.

mine the timing of branching of lineages owing to changing rates of evolution through time. For this, only the fossil record is useful.

Orangutans, chimpanzees, and gorillas differ anatomically and behaviorally from modern humans in a variety of ways. The fossils document the antiquity of some of the anatomical differences and by inference the behavioral ones. For those characters for which there is a historical record, the process of hominization was extremely gradual.

Extremities and locomotion. Living apes are primarily forest-dwelling arboreal creatures. In the trees they are agile climbers and commonly suspend themselves by their arms under tree limbs while feeding and during locomotion. In conjunction with their arboreality, they have an opposable big toe on their foot, allowing them to grasp tree limbs for support. A short, broad thorax brings the elongate arms to the side of the body. These and modifications of

the wrist, elbow, and shoulder joints greatly enhance reach and mobility of the arms, a requirement for suspensory activities. Also, the fingers of apes are long and curved, allowing the hand to operate somewhat like a hook during forelimb hanging. Orangutans are the most specialized of the apes for the arboreal mode of life. They are deliberate climbers. Their hindfoot is greatly modified as a hooklike appendage by reduction of the big toe; the range of movement at the hip joint is greater than the other apes, perhaps enhanced by loss of the round ligament of the femur. Their arms are even more elongate and their fingers more curved than those of the African apes, allowing greater reach and improved grasping ability. When they do come to the ground, living apes walk on all fours. The long, curved fingers are often or habitually brought into a fist or are turned so that the weight of the body is transmitted through the knuckles.

Human beings are of course terrestrial creatures walking bipedally. Modification of the human foot such that the big toe is no longer opposable, reorganization of the structure of knee and hip, and shortening of the fingers and arms are hallmarks of bipedalism. Based on these anatomical characters, bipedal locomotion had been achieved in *Australopithecus* at least by about 3.5 m.y. ago.

Feeding: dental and jaw structure. The living apes are almost completely herbivorous, although there is a great deal of difference among the species as to which plant parts are preferred. Gorillas prefer to eat more fibrous plant foods such as leaves, bark, buds, and pith. Chimpanzees, in marked contrast, specialize more in fruits which tend to be lower in total fiber. Orangutans have a mixed frugivorous-folivorous diet, showing great swings in preference in the wet and dry seasons. They prefer to eat fruit when available. More than any other living ape, orangutans will eat very hard-shelled fruits and nuts. The adaptations for these different herbivorous diets are reflected in the structure of the cheek teeth (molars and premolars). Compared with other apes, gorillas have more crown relief on their teeth, reflecting the comparatively well-developed cutting edges. A similar adaptive design is seen among most mammals which primarily eat fibrous foods. Chimpanzees and orangutans have comparatively low relief on their molar crowns; these flattened crown surfaces are more effective in crushing and pulping fruits with less fibrous cell walls. Orangutans have somewhat thicker cheek-tooth enamel than chimpanzees or gorillas, reflecting their abilities to open much harder-shelled fruits and nuts.

The upper incisors of the apes are spatulate-shaped devices used for separating pieces of food before chewing. This activity is accomplished either by a stripping action or by cutting against the lower incisors. The relative size of the incisors reflects the role they play in the different diets of the living apes. The more fruit-eating species, chimpanzee and orangutan, have relatively much larger incisors than does the gorilla.

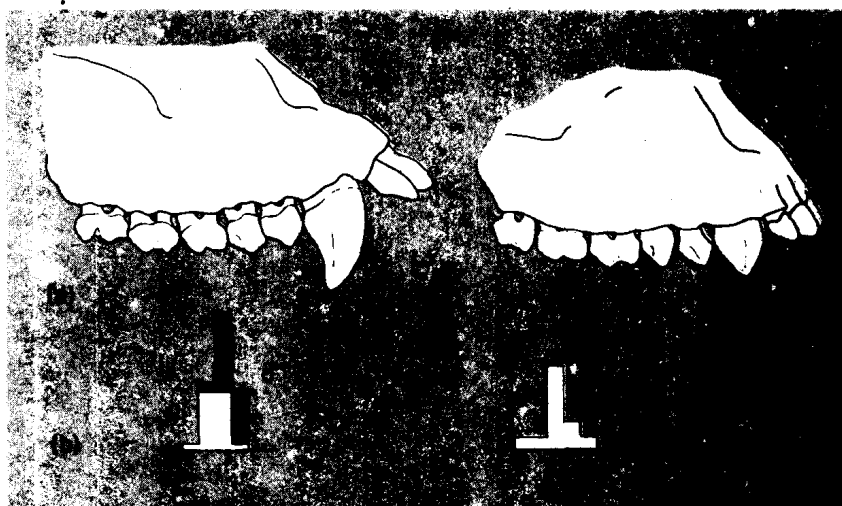


Fig. 6. Sexual dimorphism as seen in *Gorilla*. (a) Side views of the upper jaws of a male (left) and female (right) showing the larger canine tooth of the male. (b) Histograms showing the differences of molar size (left) and canine size (right). Sexually nondimorphic male molars (shaded part of histograms) overlap those of females in size, whereas sexually dimorphic male canines are always smaller.

All the great apes have large projecting canine teeth which they use to defend themselves and for threat and aggression in a sexual context. The canines are "sexually dimorphic"; that is, those of males are much larger than those of females (Fig. 6) of the species, which goes along with a higher degree of sexual competition among males. The canines of both sexes are also important tools for feed-

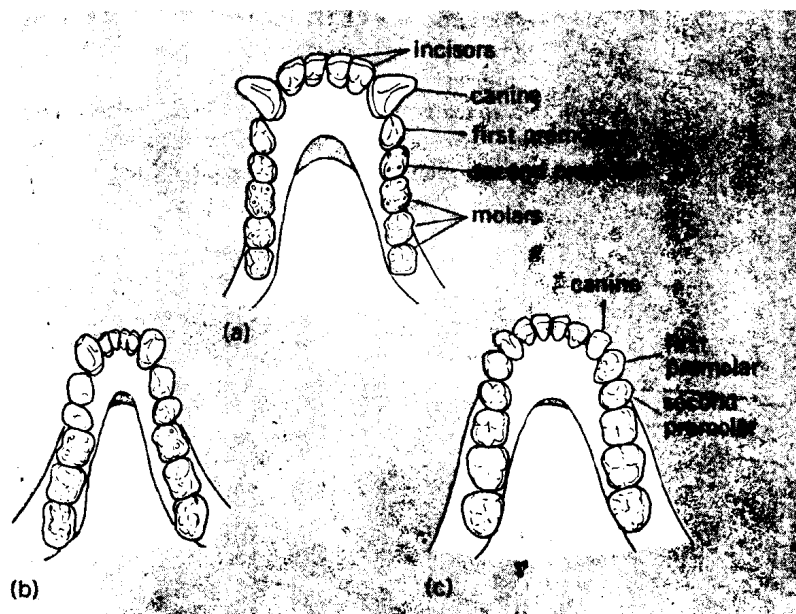


Fig. 7. Comparison of the lower jaws and teeth of (a) chimpanzee, (b) *Sivapithecus*, and (c) *Australopithecus*. The tooth rows of chimpanzees are straight-sided and U-shaped, whereas those of *Sivapithecus* are divergent and V-shaped and those of *Australopithecus* are slightly divergent and U-shaped. The incisors of chimpanzees are relatively much larger than either *Sivapithecus* or *Australopithecus*. Note also that the canines of *Australopithecus* are small and that chimpanzees have differently shaped premolars whereas in *Australopithecus* they are more similarly shaped.

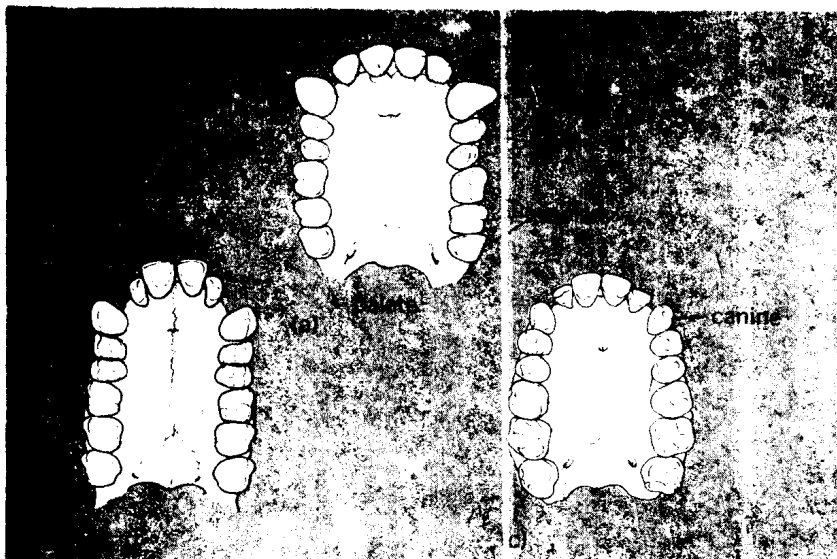


Fig. 8. Comparison of the upper jaws and teeth of (a) chimpanzee, (b) *Sivapithecus*, and (c) *Australopithecus*. Note that chimpanzees and *Sivapithecus* have large canines and straight-sided postcanine tooth rows, whereas *Australopithecus* has small canines and the postcanine teeth are bowed outward.

ing. In this context the upper canine, which is oval in cross section from front to back, contacts the front and outside face of the first of the lower premolars, thereby forming a cutting edge and sharpening device. Thus, the first and second lower premolars are very differently shaped, or heteromorphic, among apes: the first is elongate usually with a single cusp; the second is two-cusped (Fig. 7).

The shape of the palate of the living apes reflects the large size of the canines (Fig. 8). The canine, premolar, and molar teeth of apes are roughly parallel to one another on opposite sides of the palate; a space often occurs in front of the upper canine for the receipt of the large projecting lower canine. Incisors complete the U-shaped arrangement of the teeth in the palate.

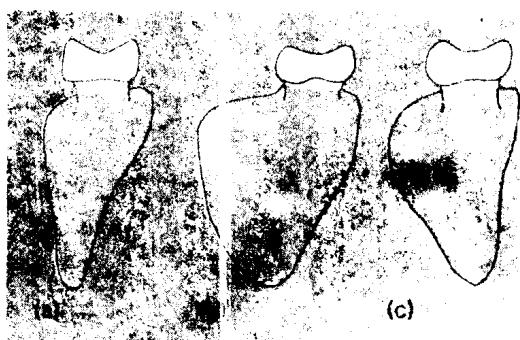


Fig. 9. Cross sections of the lower jaws of (a) *Pan troglodytes* (chimpanzee), (b) *Australopithecus* from Ethiopia, and (c) *Sivapithecus indicus* from Pakistan. *Sivapithecus* more nearly resembles *Australopithecus* in having a relatively thicker mandible when jaw depth is held constant. Sections are made through the jaws between the first and second molar teeth.

The lower jaws of the apes are deep or narrow under the molars; in cross section the distance between the base of the teeth and the bottom of the jaw is much greater than the dimension at right angles to this (Fig. 9). The midline region of the lower jaw, called the mandibular symphysis, is very deep; the dimension from the incisor margin to the back of the symphysis is much greater than the dimension at right angles to this (Fig. 10).

The dental and jaw structure of Plio/Pleistocene *Australopithecus* presents a sharp contrast with that of living apes. *Australopithecus* has extremely thick molar enamel, much thicker than any ape, and low

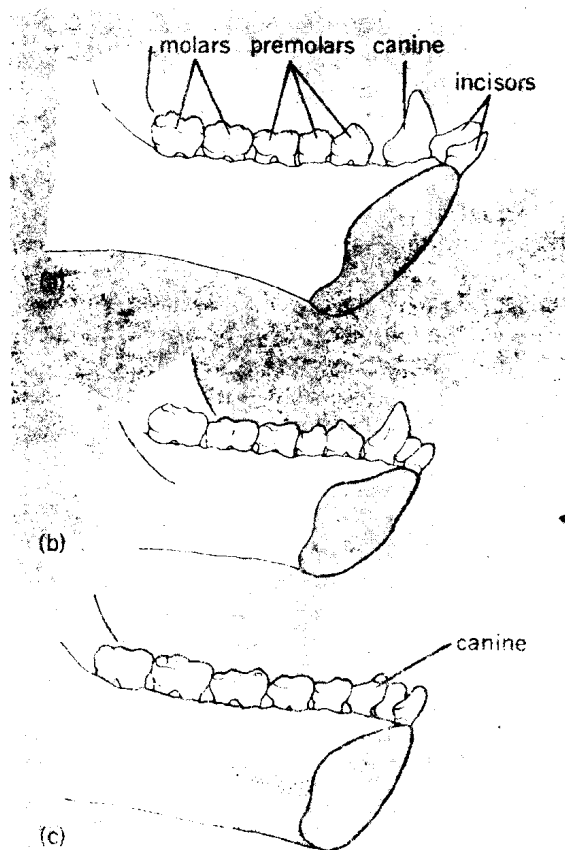


Fig. 10. Internal views of the mandibles of (a) *Pan troglodytes* (chimpanzee), male, (b) *Sivapithecus sivalensis* from India, and (c) early *Australopithecus* from Ethiopia. Each jaw has been cut in the midline to show a cross section of the mandibular symphysis (shaded area). Note the longer, narrower symphyseal cross section of the chimpanzee as well as the small size of the canine in *Australopithecus*.

crown-surface relief. The canines of this early hominoid are very small (Figs. 7, 8, 10, and 11), and there is little discernible difference between males and females. The structure of the front lower premolar is much more similar to that of the back premolar (Fig. 7) because it is no longer designed to fit against and sharpen a very large upper canine (a second cusp is generally present on the front premolar as on the second one). With the great reduc-

Table 2. Geographic and temporal distribution of large apes and prehumans over the past 20 m.y. up until about 3 m.y. before present

Species	Geographic Distribution	Temporal Range (m.y.)
<i>Aegyptopithecus</i>	Egypt	30-23
<i>Proconsul</i>	Kenya, Uganda	23-17
<i>Limnopithecus</i>	Kenya, Uganda	23-17
<i>Dendropithecus</i>	Kenya, Uganda	23-17
<i>Micropithecus</i>	Kenya, Uganda	23-17
<i>Australopithecus</i>	Ethiopia	17-3
<i>Sivapithecus</i>	Greece	10-3

tion in size of the canines the palate converges more toward the front than in the apes (Figs. 8 and 11). The lower jaw under the molars is comparatively shallower or thicker in cross section than in apes, and the symphysis is short and thicker as well (Figs. 9 and 10).

EARLY APE HISTORY

The earliest record of ape and human ancestors is found in Egypt in Oligocene times, about 30 m.y. ago. Forms like *Aegyptopithecus* resemble apes in the structure of the teeth, but are very primitive in their limb structure and most closely resemble some of the living New World primates like the howling monkey. *Aegyptopithecus* may be close to the ancestry of both Old World monkeys and apes (Fig. 5). By the early Miocene period, about 23-17 m.y. ago, the earliest Old World monkeys and contemporary apes are known. These come mainly from Kenya and Uganda. The apes are given many names, including *Proconsul*, *Limnopithecus*, *Dendropithecus*, and *Micropithecus* (Table 2). They are still quite primitive in their limb structure, but are very like modern apes in tooth structure. These African apes are best represented by specimens clus-

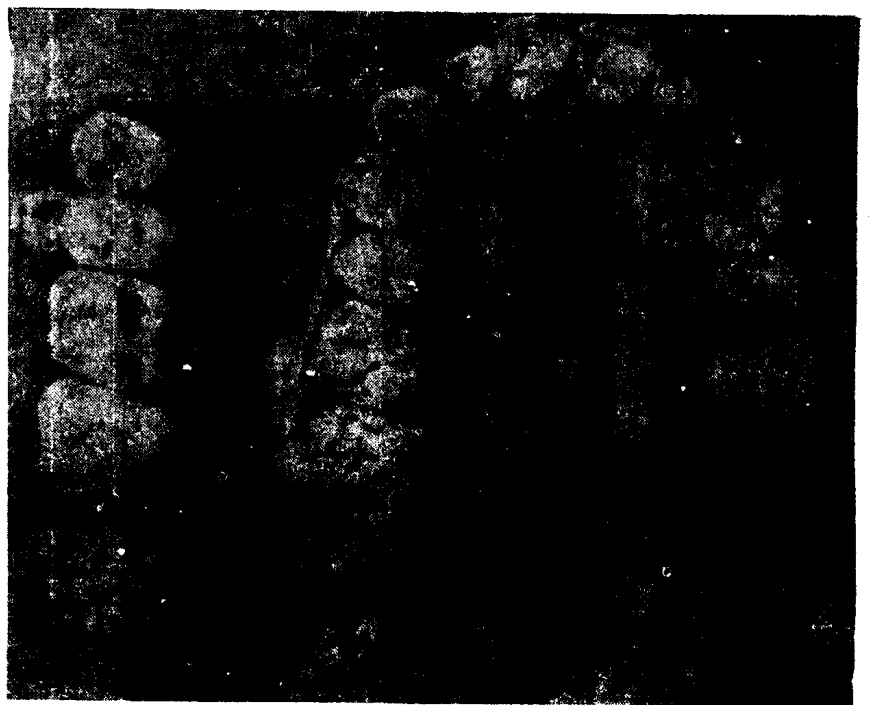


Fig. 11. Palate of an early *Australopithecus* from Ethiopia beside five cheek teeth of a *Sivapithecus* from Greece. Although separated from one another by 10 m.y., the two show remarkable anatomical similarities, implying an ancestral-descendant relationship. Both photographs, to the same scale, are of casts.

tering around 20 m.y. old; thereafter the record of their occurrence becomes increasingly scrappy and inconclusive. However, *Proconsul*, *Limnopithecus*, and their allies survived in Africa until at least as recently as 14 m.y. ago.

At around 17 m.y. ago a land link was established between Africa and Eurasia, and this allowed several ape groups to reach Europe. One descendant of the *Proconsul* group which reached Europe at least 15 m.y. ago was *Dryopithecus* (Fig. 12). *Dryopithecus* survived in Europe and southern Russia until about 10 m.y. ago. Available bones of *Dryopithecus* show considerable advances over those of *Proconsul* toward the condition seen in modern apes, especially in the structure of the jaw, face, and arm bones. Although known *Dryopithecus* are contemporaries of earliest ramapithecines, the latter are probably descendants of a form like *Dryopithecus*. Ramapithecines, which are similar to *Dryopithecus* in many ways but differ in possessing very thick tooth enamel, first appeared in Africa and Turkey about 15 m.y. ago (Table 2 and Fig. 13). By about 10–8 m.y. ago they had spread widely in Eurasia, reaching Austria, Hungary, Greece, India, Pakistan, Nepal, and China, as well as continuing to exist in Turkey and Africa. Thereafter the spread of more open country with the decline of the forest regions, as well as climatic cooling, led to the virtual extinction of Eurasian *Dryopithecus* and ramapithecines; after about 8 m.y. ago, only *Gigantopithecus* survived in this once diverse larger ape community. *Gigantopithecus* has been recovered in caves dated as recently as 5 m.y. ago.

The poor quality of the African fossil record after about 17 m.y. ago has been alluded to in the above discussion. This is particularly true for the period between 10 and 6 m.y. ago, a time which is critical for clarifying the course of human evolution because

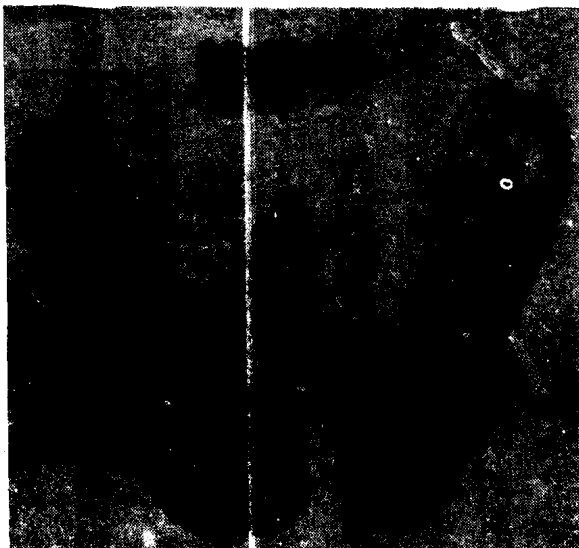


Fig. 12. Several views of a lower jaw of *Dryopithecus* from northern Spain. Left, a bottom view of the jaw; right, a top view with three molars shown; top, a side view of the cheek teeth; middle, a detail of the inside of the mandibular symphysis. (From A. S. Woodward, 1914)

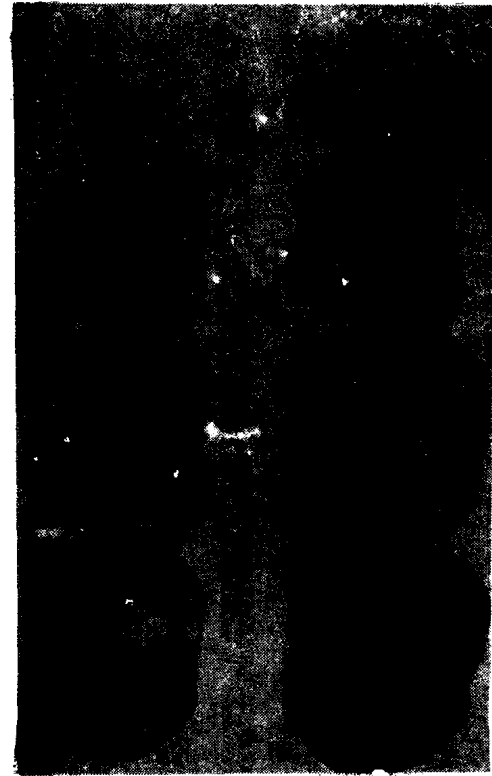


Fig. 13. Lower cheek teeth of (a) *Dryopithecus* from Spain with three molars, and (b) *Sivapithecus* from India with one premolar and three molars, the first of which is broken. The front of the jaw is at the top. In both specimens, the enamel has been worn while the animal was alive, so that the dentin shows in several places. A star identifies one such place. The three molars developed and erupted in sequence from front to back. The gradient of wear is much more in the *Sivapithecus* jaw than in *Dryopithecus*. Note that enamel is much thicker in *Sivapithecus* than *Dryopithecus* at the points indicated by the arrows.

Australopithecus, the first bipedal hominid, evolved in Africa in this period. In this time interval only two isolated ramapithecine teeth are known from the whole continent of Africa. These are sufficient only to establish continuity between thick-enamelled ramapithecines and the first thick-enamelled *Australopithecus*, which was found at Lothagam in Kenya from sediments dated at about 5 m.y. ago.

RAMAPITHECINES IN HOMINID EVOLUTION

Currently there are three views as to the place of ramapithecines in human and ape evolution. Some researchers believe ramapithecines to be the ancestors of great apes and man. Others have emphasized some similarities of ramapithecines to the orangutan and argue for a close phyletic relationship between the two. The last and strongest documented view is that ramapithecines are more closely related to man than to any of the apes.

Ancestors of apes and humans. The first view, that ramapithecines are the ancestors of all living greater apes and humans, is currently propounded most strongly by the American anthropologist L. O. Greenfield. Greenfield has correctly noted that sup-

posed resemblances between ramapithecines and *Australopithecus*, the earliest undoubted hominid, have been greatly exaggerated (and in some instances are purely fanciful). For example, there is no evidence that ramapithecines were bipedal or had small canines like *Australopithecus*, as claimed by some (Fig. 8). At the same time he views ramapithecines as bearing a great adaptive and phenotypic resemblance to living apes. From this, and his view that humans passed through an evolutionary stage where they looked like living great apes, Greenfield believes that ramapithecines may be ancestral to both apes and humans. Greenfield is right that ramapithecines show several resemblances to living great apes no longer found in modern humans. For example, the structure of the ramapithecine foot is more like that of living apes than humans, as is the overall shape of the facial bones. However, such similarities are most likely holdovers from the last common ancestor of great apes and man, and it is to be expected that the earliest member of a human lineage would resemble its ape ancestors in most ways. However, the important point is that, as will be discussed below, ramapithecines show certain key changes which point to the beginnings of human trends and suggest that the human lineage began with the ramapithecines.

Orangutan ancestry. The second view, currently propounded most strongly by the British paleontologist Peter Andrews, is that many features of the anatomy of *Sivapithecus* greatly resemble those of the orangutan, so *Sivapithecus* may be closer to orangutan ancestry than to that of man. Andrews mentions a number of details of the structure and shape of the face of *Sivapithecus*, particularly of specimens from Turkey (Fig. 3) and India, which resemble orangutans. Both have tall, oval-shaped orbits with a narrow bony bridge between them, and weak brow ridges above and between the orbits. In both, the upper face is flattened and flares outward; both have a much larger middle than outer upper incisor and thickened enamel on the molar teeth. At first glance, these resemblances might appear to establish this relationship, but study of the facial structure of early Miocene apes, *Australopithecus*, and living apes gives several plausible reasons why they may be insubstantial. The weak brow ridges of *Sivapithecus* and the orangutan are possibly what one might expect in the common ancestor of man and all great apes, given that early Miocene *Proconsul* has weakly developed brow ridges as well. A number of other *Sivapithecus*-orangutan similarities mentioned by Andrews are seen also in early *Australopithecus* and could be used with equal vigor to indicate a *Sivapithecus*-*Australopithecus* phyletic link. This includes the flattened, outwardly flaring upper facial bones, the much larger central than outer upper incisor, and the thickened enamel on the molar teeth. Finally, *Sivapithecus* and *Australopithecus* have much thicker enamel than do orangutans, suggesting that the latter evolved thick enamel independently in parallel with *Sivapithecus*.

This leaves the shape and disposition of the orbits as unique resemblances between *Sivapithecus* and orangutans which are not found in *Australopithecus*. However, other impressive and unique similarities point to a *Sivapithecus*-*Australopithecus* link, making it more plausible to assume that the oval orbit shape and narrow interorbital bony bridge evolved convergently between *Sivapithecus* and *Australopithecus*.

***Australopithecus* and *Homo* links.** The third view, advocated here, is that ramapithecines may be specially related to *Australopithecus* and *Homo* and not to other living or fossil groups. The similarities between *Sivapithecus* and *Australopithecus*, as distinct from modern apes, are illustrated in the accompanying figures. *Sivapithecus* resembles *Australopithecus* uniquely in the following ways (Figs. 7-11). (1) Each has a thick or shallow lower jaw under the molars and at the mandibular symphysis; in apes the jaws are narrower or deep. (2) Each has very thick enamel on the cheek teeth; apes, even orangutans, have thinner enamel. (3) There is a tendency to have two cusps on the foremost of the lower premolars; ape front premolars are usually single-cusped. (4) The upper canines are comparatively wider than long in cross section; in apes the greatest cross-sectional dimension is tangential to the dental arcade. (5) The canines are similar-sized in both sexes, whereas in apes they are much larger in males than in females. As will be reviewed below, these similarities show *Sivapithecus* to have shared two fundamental adaptations with early hominids—hard-object feeding and a possibly monogamous social structure. This makes the similarities more fundamental than the few resemblances of the shape and position of the orbits between orangutans and *Sivapithecus*, which are of uncertain functional or adaptive significance.

Thus, available evidence points to a link between ramapithecines and *Australopithecus*. It must always be recognized, however, that further knowledge about the details of ramapithecine anatomy could lead to a rejection of this hypothesis. Particularly vexing is the absence of informative fossils documenting the course of ape or human evolution between about 8 and 4 m.y.

RAMAPITHECINE ADAPTATIONS: LOCOMOTION

Locomotor differences are foremost among the ways by which humans and apes differ. Humans today are striding bipeds and facultative ground dwellers, while man's closest ape relatives move about on all fours in the trees. It is thought that humans passed through an evolutionary stage when they much more closely resembled chimpanzees in terms of locomotor capabilities. Precise information as to whether ramapithecines were primarily tree dwellers or spent some time on the ground, and as to their mode of locomotion, awaits further evidence about their limb structure. At present, from Pakistan there are some bits of the upper arm bones pos-

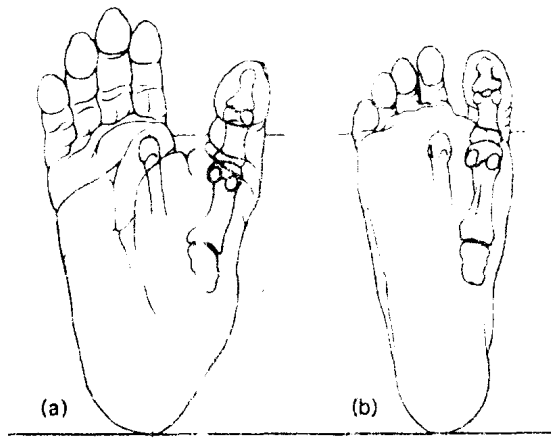


Fig. 14. Outlines of the sole of the foot of (a) a chimpanzee and (b) a human, showing the positions of the bones of the big toe and the head of the metatarsal bone of the second digit. Note that the ape big toe is a diverging grasping organ while the human big toe is in line with the other digit rays. (From A. H. Schuit, *The physical distinctions of man*, Proc. Amer. Phil. Soc., 94:428-449, 1950)

sibly of *Gigantopithecus* and of a large *Sivapithecus*. The latter is also known from fragments of the hand and a few pieces of the bones of the leg, ankle, and foot. The ankle and foot bones are the most informative so far. The joint surfaces give some information about the sorts of movement which could be made. *Sivapithecus* could turn its ankle inward freely, as can the living apes, and to a degree not allowed in the human ankle. Also the big-toe bones of *Sivapithecus* indicate that this digit most likely served a grasping role like in the chimpanzee foot but unlike the human, where the big toe is bound by ligaments in parallel to the other digit rays (Fig. 14). All of this points to an animal which used its hindfoot to grasp tree limbs, not as a propulsive strut in the manner of a human foot. Other known skeletal parts of ramapithecines also resemble those of great apes, suggesting that *Sivapithecus* was at least as tree-living as are chimpanzees today. One may speculate that the *Gorilla*-sized *Gigantopithecus* was somewhat more of a ground dweller.

RAMAPITHECINE ADAPTATIONS: DIET

Today, hunting and gathering societies like the Kung! Bushmen of Africa eat about 20% meat and 80% vegetable food. Chimpanzees, the most meat-eating of the apes, eat no more than 2% meat; thus, human evolution has seen a tenfold increase in the importance of animal food for energy. This appears to have been a relatively recent development, however, perhaps over the last 1-1.5 m.y. It is hard to imagine how prehuman hunters could have been efficient without highly developed tools, and there is nothing to suggest that earliest *Australopithecus*, the bipedal hominids of the Pliocene and early Pleistocene, were efficient hunters. Thus, factors other than hunting must be looked for to explain the origins of peculiar early hominid dental structures and bipedalism. In fact, if it is supposed that

ramapithecines are the ancestors of *Australopithecus*, some hominid dental adaptations preceded hunting or meat eating by up to 10 m.y. As mentioned above, the cheek teeth of ramapithecines like *Australopithecus* have very low surface relief compared with those of apes, and are covered with a very thick layer of hard enamel, unlike those of most apes. Furthermore, ramapithecines resemble *Australopithecus* in that their jaws are very stout and thick, and the scars on these bones show a strong development of the muscles which provided masticatory force. All of these features point to a chewing system evolving early in human ancestry designed to produce and withstand extremely powerful chewing forces. Comparative study of the teeth of living primates and other mammals suggests an explanation for these features as adaptations for a specialized plant-eating diet.

Among herbivorous mammals a sharp adaptive dichotomy exists between browsers which primarily eat leaves and other plant parts high in fiber, and frugivores which eat fruits and other less fibrous plant parts. Browsers have specialized digestive tracts accommodating microorganisms which assist symbiotically in the digestion of plant fiber. Also browsers have well-developed cutting crests on their cheek teeth which can break up the fiber, increasing its surface area and improving digestibility. In contrast, fruit-eating mammals have relatively simple digestive systems and cheek teeth with large crushing surfaces and short, blunt, rounded cutting edges. Quantification of the development of the cutting systems on cheek teeth has been attempted. A shearing quotient (SQ) expresses the degree of enhancement of cutting edges on the unworn molars of browsing species compared to frugivorous ones. SQs for living apes serve as a model for the SQs of fossil apes and ramapithecines. SQs of chimpanzees and gibbons are near zero, as befits their frugivorous habits; SQs of the gorilla and siamang (a specialized browsing gibbon from Southeast Asia) are around 7-10, which goes along with their being browsers.

The SQs of ramapithecines cluster around zero, much like fruit-eating chimpanzees. However, it cannot be definitely concluded from this that *Sivapithecus* and *Gigantopithecus* had diets very similar to those of living chimpanzees. Certainly the relatively poor expression of cutting edges on the cheek teeth of the extinct forms suggests they ate very little fiber, like chimpanzees and unlike gorillas, but the added observation that ramapithecines have very thick enamel on their cheek teeth while chimps do not suggests some other fundamental dietary differences.

It has long been thought that the thick enamel of ramapithecines had something to do with their terrestrial habits: *Australopithecus* was a ground-dwelling biped with thick enamel on its cheek teeth. It is often assumed that ground dwelling and thick enamel evolved together so that having thick enamel could indicate terrestrial habits. In this view, human ancestors came to the ground and became bi-

pedal to exploit new foods like roots, fibers, or cereal grains. These foods, because they are hard, tough, or grit-covered, might in turn have selected for thick enamel. It is now known that this view is incorrect for two reasons. First, *Sivapithecus* was probably a tree dweller, and certainly not a biped, but had thick enamel. So human ancestors probably evolved thick enamel before they assumed a ground-dwelling habitus. Second, thick cheek-tooth enamel is found today only in primates which eat very hard-shelled fruits or nuts. Two of the best examples of the adaptive significance of thick enamel are found in the feeding behavior of the cebus monkey from South America and Sumatran orangutans, both arboreal species. Each species has been observed to break open with its teeth nuts which are so hard that other species cannot eat them, and each has very thick enamel.

Orangutans do not always eat hard nuts, however. During the dry season they are primarily browsers. This may explain why their enamel, while relatively thicker than that of other apes, is not as thick as that of the cebus monkey. Field studies of the latter suggest that it is much more committed to nut eating on a yearly basis. From all of this it is reasonable to conclude that having thick enamel is a nut-eating adaptation. Such an adaptation involves very powerful muscles of mastication, as well as very thick enamel on the cheek teeth. Once the food has been broken open, the softer pith inside has very little fiber in it so molar cutting edges are not selected; living nut feeders have low SQs and thick enamel, precisely the pattern shown by ramapithecines. There seems to be no relationship with terrestriality.

In summary, it appears that the ramapithecines, although vegetarians like living apes, were specialized in particular for eating extremely hard foods like thick-shelled forest nuts.

SOCIAL STRUCTURE OF RAMAPITHECINES

One of the greatest distinctions between man and the apes is in the canine teeth. The canines of apes are large projecting teeth, larger in males than females (that is, sexually dimorphic; Fig. 5); human canines are not projecting and there is only minimal difference between the sexes. There are good reasons for believing that humans passed through an evolutionary stage when they had larger, sexually dimorphic canines; living great apes, most monkeys, and most fossil apes have such an arrangement. Moreover, although the crowns of human canines are small, the roots are stout and long, possibly a hint that they were once larger. The canines of ramapithecines are still quite large (Figs. 7, 8, and 10), but the amount of sexual dimorphism was low by the standards of living apes. This gives valuable information about the possible social structure of ramapithecines.

Most living monkeys and apes have sexually dimorphic canines, but in a few, notably the gibbons of Southeast Asia and many New World monkeys,

the canines of males and females are similarly sized. Sexually dimorphic anthropoids form polygynous social groups with one or several adult males, a larger number of females, and their offspring. Nondimorphic anthropoids, on the other hand, form family groups composed of a single male, a single female, and their immature progeny. Therefore, ramapithecines, which have little canine dimorphism, may have had a family-type social group. From this scenario man's early preramapithecine ape ancestors had large, sexually dimorphic canines like those of living great apes, implying a polygynous social structure. Later, in the ramapithecine stage, the canines were reduced in size, giving the modern human configuration.

CLASSIFICATION

The available evidence suggests that ramapithecines are broadly ancestral to the hominids (*Australopithecus* and living humans) and not to any living ape. But in terms of their overall grade of organization, ramapithecines show a mixture of ape and hominid adaptations which on balance would make them appear quite apelike. So should ramapithecines be called hominids (members of the Hominidae, the family of man)? A satisfactory solution to this problem is elusive because it relies as much on philosophy as on the evidence of relationship. The reason the question is raised here is that it focuses on a key fact of human evolution: peculiarly human features or characteristics were not all acquired simultaneously as part of a common adaptive package. *Homo* is distinct from living apes in a variety of ways which could leave evidence in the fossil record—bipedality, tool use, enlarged brains, relatively small canines, reduced canine sexual dimorphism, and thick molar enamel are a few of the features which characterize the human adaptive "grade." As the fossil record improves, scientists are finding that some of those differences arose millions of years before others in human evolution. Human ancestors got their feet (and possibly their knuckles) very wet when they crossed the ape/human adaptive Rubicon, and this makes a definition of the family Hominidae extremely arbitrary. Should only those human ancestors who were bipeds (or tool users, or large brained) be included in the human family? The alternative, which R. Kay leans toward, is to define the human family as containing all creatures, no matter how apelike, that are more closely related to *Homo* and *Australopithecus* than to any of the living apes. By this definition ramapithecines should be included in the human family.

[RICHARD F. KAY]

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FT. Sherman

Autofacturing

Autofacturing—automation in manufacturing—is a term to describe the overall activities of the automated factory. The 10 major components of a total autofacturing system are: product design for autofacturing, data-base construction and management, integrated computerized control system, automated materials-handling system, process and machine automation, automatic assembly machines, robots, automatic inspection and testing system, automatic maintenance system, and human interfaces with autofacturing.

Each of these components may be thought of as a subsystem of the total autofacturing system, and each, in turn, contains its own subsystems. The presence of all 10 is not required to have an autofacturing system. Each is presently in its own stage of development, and autofacturing may exist as a mixture of some advanced subsystems operating next to some which are less sophisticated. The ultimate goal should be to have all subsystems interconnected, complementary, and integrated into an overall autofacturing system in order to achieve the greatest possible benefits. It is expected, however, that advances will continue in each area, keeping the perfect total system a future target.

Autofacturing is not manufacturing—it is its technological successor. The term manufacturing was originally defined as the making of a product by hand; then it was expanded to include the making of a product by machinery. The word auto-

Vincent M. Altamuro became the president of Management Research Consultants in 1955. Formerly on the faculties of the graduate schools of engineering of Columbia University and The City University of New York, he has conducted seminars for Western Electric, the manufacturing subsidiary of AT&T, for over 20 years—one of the courses being in autofacturing, a term he originated.



mation is used to describe a wide range of activities, some not at all related to industrial plant operations, for example, airline reservations, banking, stock market transaction handling, traffic control, commercial data processing, word processing, and office automation. Recognizing the foregoing, V. M. Altamuro originated the word autofacturing to create a term which more accurately describes the activities of the factory of the future in which the products will not be made by hand but by automatic, self actuated, computer-controlled machines, robots, and self-correcting feedback equipment.

The advantages of a fully operational autofacturing installation include greater output and lower per-unit costs, that is, increased productivity. Also to be expected are improvements in quality—more uniform, consistent output, with less handling damage, fewer rejects, and less scrap and rework because of continuous monitoring and rapid corrective feedback. It should also result in fewer personnel, reduced payroll expenses, fewer accidents, less material handling, less inventory, and reduced space requirements. One disadvantage is that its high output rate may be an all-or-nothing situation. That is, if the system breaks down, output could drop to zero. This problem can be lessened by designing the system to be compliant and flexible. The feature of compability means that the system contains the ability to continue operating when a tool or work station breaks down (by using rerouting or redundancy) or varies in output rate (by using work-in-process accumulators). Flexibility refers to the ability of the system to adapt quickly to desired changes in products, output rates, mixes, and other specifications. The use of group technology—the coding and grouping of parts according to similarities in their sizes, shapes, materials, and production processes—may be an aid in this regard for products with shorter production runs. Another consideration is that the higher capital investment required for the installation raises the operation's break-even point. Also, while autofacturing requires fewer personnel, those remaining (engineers, computer specialists, and maintenance technicians) require a higher level of training, skill, and salary.

There are two basic ways in which autofacturing may be installed in a company. It may be installed "from scratch" in a new or remodeled facility or for a new product line in an existing facility. Or, it may be installed in sections as the technology, available capital, timing, and other circumstances allow. Then, at a later date and after the individual sections are debugged, these "islands" or "cells" may be connected and integrated into a total autofacturing system.

A brief description of the elements and state of the art of each of the 10 components of a total autofacturing system follows.

Product design for autofacturing. The first essential of an efficient autofacturing system is that the product—including its component piece parts and

raw materials—be designed and specified so as to aid the system. That is, without detracting from the performance requirements, certain things can be done, at the product design stage, to permit a higher degree of efficient autofacturing.

Product. The product should be designed for modular assembly with simplified subassemblies. This means that rather than having it designed to be built by continuously adding part after part, it is designed to have a set of more simple subassemblies which, when brought together, become the end product. In addition, the subassemblies should be modular in such a way that various interchangeable combinations of them create different end products.

Piece parts. In autofacturing, the piece parts are handled by parts feeders, mechanisms, robots, and other nonhuman devices. They must be designed so that they are as simple, uniform, symmetrical, and sturdy as possible. The devices used to hold, sense, count, orient, feed, position, fixture, and assemble them must operate quickly and surely. The parts must not tangle, snag, nest, or shingle (overlap). They must not break or damage easily. They must have (or be given) features which make them easy to sense, move, and hold automatically and without error. An autofactured part or product may have features which have no function in the end product but exist merely to make it easier to handle the product as it flows through the autofacturing system. Also, the component piece parts should be designed so as to have as few at-rest orientations as possible. That is, a sphere has one orientation and is therefore always oriented properly; a coin has two (it may fall heads or tails). As parts become more asymmetric, irregular, and complex, they have an increasing number of possible orientations, making it much more difficult to get them into the orientation required at the next stage of the process.

Raw material. The raw material should be specified so as to be received from the suppliers in a form best suited for introduction into the autofacturing stream. The form, size, shape, packaging mode, and even the time and point of delivery can often be varied so as to best fit the requirements of the subsequent steps.

Data-base construction and management. For a true totally integrated autofacturing system, there must be a common data base. This means that all information used by and created by the system and its subsystems must be coded, structured, and organized in such a manner that it can be collected, stored, interpreted, processed, updated, retrieved, displayed, and communicated between and among the many elements of the overall system.

The data must be collected from the points where they originate and delivered to the points where needed. Some devices and media of data transmission are magnetic strip, bar code and alphanumeric scanners, keyboards, light pens, magnetic wands, touch-sensitive CRTs (where the displayed data touched are entered into the data base), voice, hand-held portable terminals, radio waves, line-of-

sight light beams, lasers, fiber optic light guides, and the plant's standard 120-V electric power wiring used to carry data.

The data base could begin with the design engineer feeding a new product's specifications into the computer. The detail designer would retrieve them, specify exact dimensions, components, and hardware, and add those data to the base. The drafter would use that information to prepare the engineering drawings; then the information would be used for the preparation of parts lists, bills of material, exploded views, and so on. The engineering data would be an input to production information needed for the preparation of numerical control tapes and programs, work routings, machine loading, and so on. Subsequent design changes would be made by updating the original data, wherever located throughout the system. The principle is that one common set of data, once created, is kept current and used by all persons and functions of the organization.

The term distributed data-base management system is used to describe a data-base management system in which the data are collected from and distributed to different locations. The required data-base management system may be designed internally by the firm installing autofacturing, or it may be acquired from the vendors of computer program packages.

Integrated computerized control system. An autofacturing installation will not operate properly without an integrated computer system. The computer hardware can be any mixture of full-size mainframes, minicomputers, and microprocessors and microcomputers. Even the "intelligent" programmable controllers may be included. The firmware and software can be designed to perform the functions of computer-aided design and drafting, computer-aided design/computer-aided manufacturing (CAD/CAM), computer-aided engineering, computer-aided process planning, the planning and control of master schedules, material requirements planning, inventory control, tool control, machine controls, numerical controls, quality analysis and control, statistical analysis of data collected, data-base management systems, and management information systems and reports.

Automatic information feedback and control are essential to autofacturing. The system must operate at speeds too high to permit periodic measurements of conditions, human reactions, evaluations, decisions, and manual adjustments to bring conditions back to desired levels. In the time that the human or manual sequence would take, a multitude of substandard products could be made, an entire production batch ruined, or worse, the equipment seriously damaged. A closed-loop automatic control system continuously monitors key parameters, com-

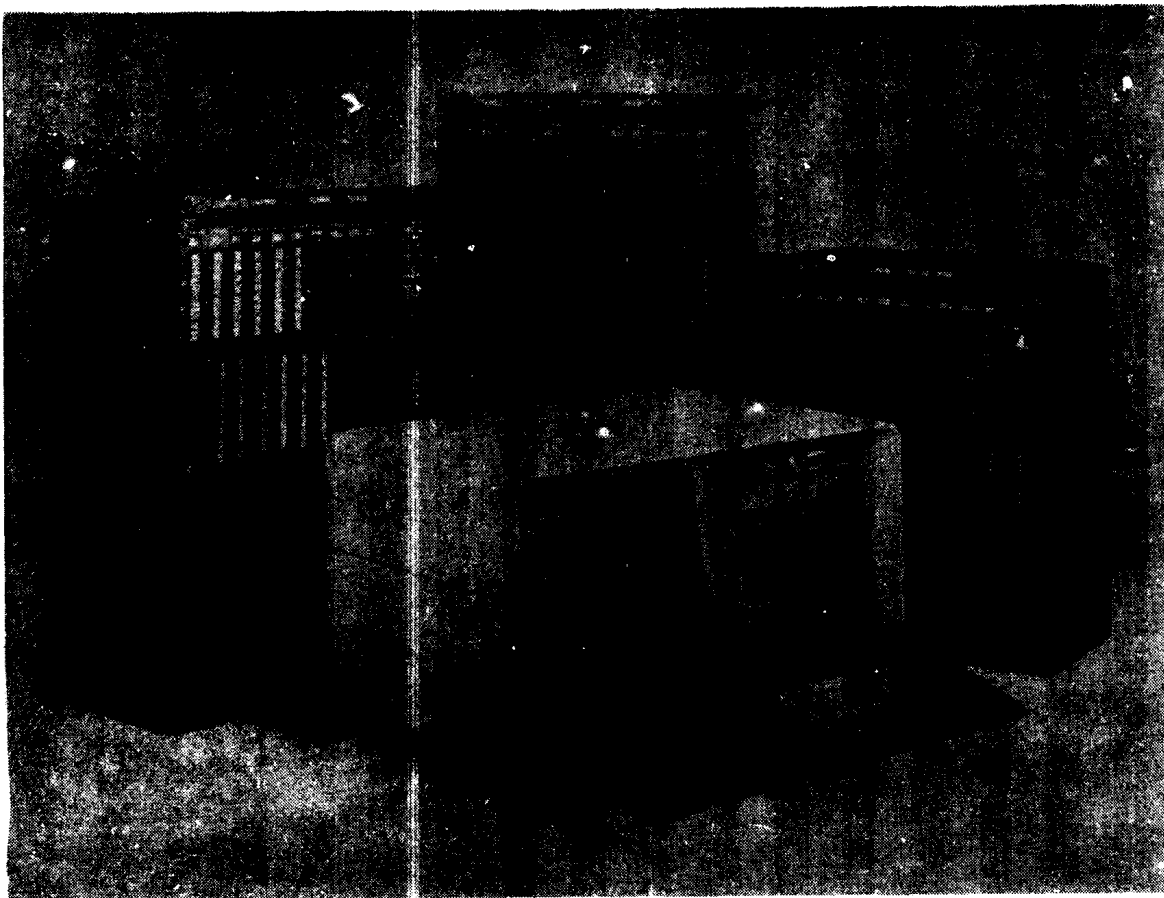


Fig. 1. Microprocessor-based programmable controller. (General Electric Co.)

compares them to standards, computes a difference or correction signal, feeds it back to the input stage, and actuates adjustments to keep the process within preestablished limits—all so rapidly that no substandard products are made.

In autofacturing, most operations are under the complete direction of a computer—either from a remote location or right on the factory floor, possibly built into the machines. In addition, auxiliary devices such as programmable controllers (Fig. 1) and logic sequencers are handy enough for the factory floor environment and are becoming sophisticated enough to perform computer functions. The programmable controller's place in the factory is that of an interface between the machine and the central computer. The programmable controller is used to direct the machine's operations and then to monitor and feed back the results to an information and control computer—which might have dozens of programmable controllers hooked into it.

The autofacturing computer system may be centralized (a large computer with many remote input/output terminals throughout the plant), or it may be a distributed system (microcomputers and programmable controllers at each location tied to supervisory minicomputers which, in turn, interface with the maxicomputer). Also, the system may be networked in a hierarchy, such that the computers (of all sizes) are connected so that information can flow from work stations to machine centers, to departments, from the plant shop floor to the functional offices, up to corporate headquarters. Remote computer CRT terminals, interactive graphics, and digital input and readout stations are all components

of the integrated computerized control system. Artificial intelligence, voice communications with machines, and natural language programming of computers are developing and will find their place in future systems.

Automated materials-handling system. Beyond the conventional materials-handling equipment and systems of today's factories, the factory of the future operating in an autofacturing mode will also have programmable conveyors, computer-directed forklift trucks, automatic guided vehicle systems, and automatic storage and retrieval systems (AS/RS).

Conveyors. In autofacturing, conveyors will be programmed and instructed by control signals to switch paths, change speed and direction, accumulate work, release previously accumulated work, read bar codes, sense items, and react accordingly. The actions of the conveyors will be tied to inputs from a real-time information system and, in turn, will feed current data back to central control.

Forklift trucks. Computer-directed forklift trucks are already in operation and are growing in use. Their operation is not completely automatic in that a human operator is still required, but they do represent an additional step toward the automatic factory of the future. The installation consists of a central computerized base station and trucks equipped with an FM radio transceiver, a microprocessor data terminal with a liquid crystal or light-emitting diode display screen, an alphanumeric input keyboard, and in some cases, an electrostatic printer. This two-way real-time data flow reduces errors, time, and some personnel—although a truck operator is still required. In operation, coded signals are trans-

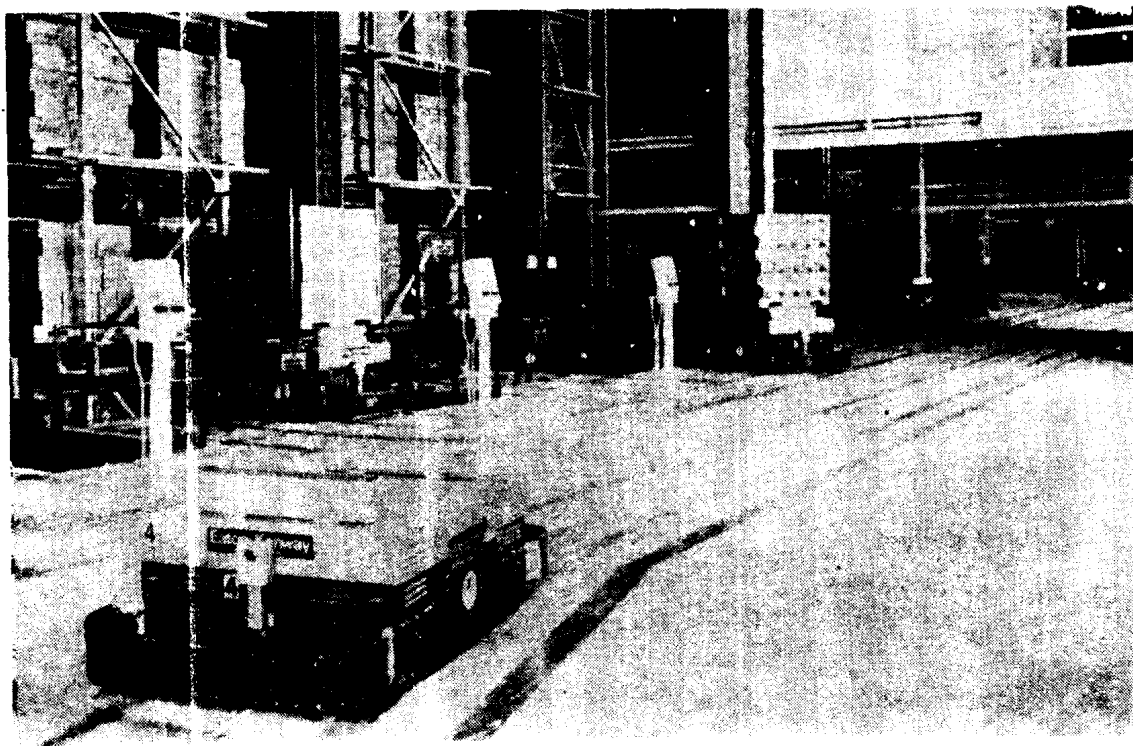


Fig. 2. Kenway RoLocarrier automatic guided-vehicle system. (Eaton Corp.)