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Primates

Recent studies have provided new information on the most ancient phases of human ancestry and on the early development of human cultural traits.

HUMAN ORIGINS

The order Primates, including the living squirrel-like "prosimians," monkeys, apes, humans, and their diverse extinct relatives, has a long history. The earliest known fossil primate, *Purgatorius* (represented by one tooth), lived alongside the last dinosaurs in Montana some 65 million years (MY) ago. Since then, many distinctive lineages have evolved and adapted to diverse modes of life, including human life. The evolutionary history of this group is thus of interest not only as a scientific exercise, but for what it might tell about the processes which formed the human species. Recent advances have been made in many areas of this history, especially in knowledge of

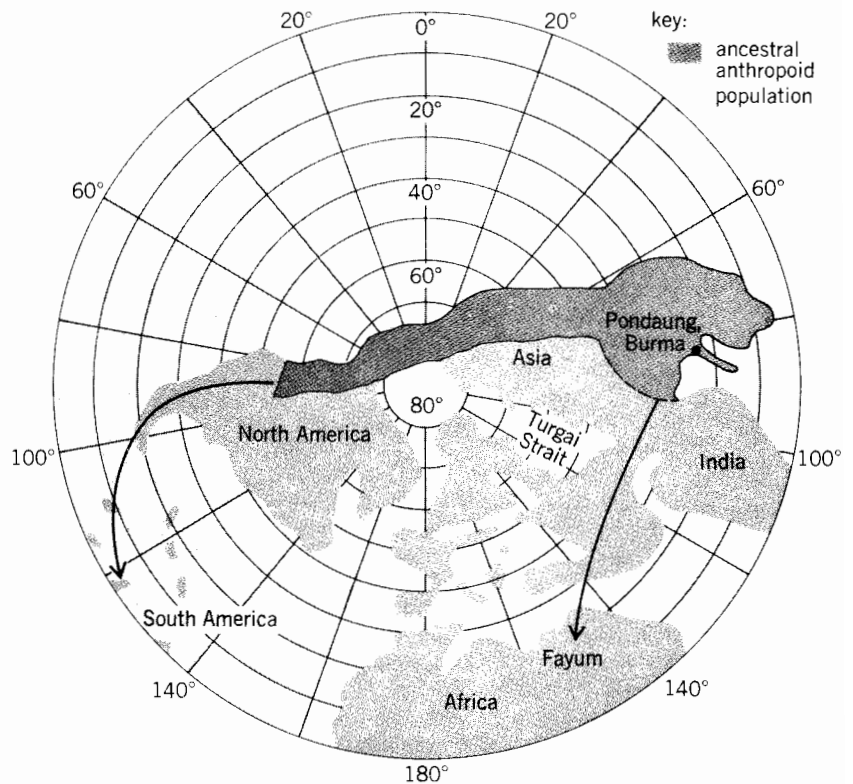


Fig. 1. Late Eocene continents and possible early anthropoid dispersal.

three groups of animals which may have been close to the origin of humanity.

Today there is a consensus (strongly opposed by some active scholars) that the living tarsier of Southeast Asia is the lower primate most closely related to the anthropoids (higher primates: monkeys, apes, and humans). Fossils widely accepted as related to tarsiers first occurred in North America and Eurasia at the start of the Eocene Epoch, 54 MY ago, diversifying and then dying out over the succeeding 30 MY. The earliest anthropoids are known from the southern continents of South America (Bolivia) and Africa (Egypt) early in the Oligocene Epoch, about 34-30 MY ago. These latter anthropoids are already members of the two geographically distinct modern anthropoid subgroups Platyrrhini and Catarrhini, from the New and Old Worlds, respectively. A still older primate known as *Pondaungia*, from the late middle Eocene (about 40 MY ago) of Burma, had sometimes been suggested as a possible anthropoid, but it was represented only by damaged fragments of teeth. New, slightly more complete finds of this animal appear to confirm its anthropoid status, in fact indicating that it was already a protocatarrhine. If so, it would appear that the circumpacific lands played a larger role in anthropoid dispersal than is usually acknowledged (Fig. 1).

Increased understanding of plate tectonics and the past positions of the continents has promoted the theory that anthropoids arose in (or near) Africa and divided into the two subgroups known today. Ancestral platyrrhines then drifted to South America on rafts of natural vegetation masses, following the past currents deduced from deep-sea fossils. But no African catarrhine fossil is a likely

ancestor for platyrrhines, the two groups being morphologically distinct from their earliest occurrences. If, however, a group of protoanthropoids evolved in eastern Asia or western North America during the early Eocene from known tarsier-like ancestors, its descendants might have crossed the Bering Straits to form a circumpacific distribution. The protoplatyrrhines might then have entered South America from the north via the tectonically unknown Caribbean region, while protocatarrhines (such as *Pondaungia*) expanded west and south to cross the Tethys seaway separating Africa from Asia. Just as *Pondaungia* is most similar to some Egyptian early catarrhines, representatives of other mammalian groups have a fossil distribution which suggests that Burma-Pakistan-(Turkey?)-Egypt was a plausible route of migration and expansion of range in the later Eocene. The actual crossing of the Tethys barrier might have been simplified by an apparent world-wide(?) lowering of sea level at the end of the Eocene.

Oligocene early catarrhines. Recent expeditions to the richly fossiliferous Fayum beds of Egypt have greatly expanded knowledge of the collateral relatives of *Pondaungia*. In addition to clarifying some points of taxonomy (and, as usual, clouding others), this research has confirmed the essentially monkeylike nature of the locomotor system of all the Fayum catarrhines. What is intriguing, however, is that the monkeys which offer the closest comparisons are not those of Africa or Asia, but instead the platyrrhines of the New World. The latter thus appear to have retained many of the features of limb bone function which characterized early catarrhines, and, presumably, their common anthropoid ancestors. *Propliopithecus* (or *Aegyptopithecus*), the Fayum form most like *Pondaungia* dentally, may have already begun a trend to increased use of the forelimb for support and locomotion which culminated in the modern apes (and the ancestors of humans). Moreover, *Propliopithecus* (and other Fayum forms as well) appears to have been characterized by a pronounced degree of sexual dimorphism in both canine tooth size and lower jaw proportions, indicating significant differences in adaptation between the two sexes. Elwyn Simons and his collaborators have taken these morphological features as indicators of a polygynous, rather than monogamous, social system, by analogy with modern higher primates. See AEGYPTOPITHECUS AND PROPLIOPITHECUS.

Early Miocene hominoids. A gap of several million years separates the Fayum forms from the succeeding *Dryopithecus* group of early hominoid species. The Hominoidea, or humanlike (rather than monkeylike) catarrhines, are now generally considered to include a conservative family Pliopithecidae, for the Fayum "apes" and some younger relatives, and one or two families (Hominidae and perhaps Pongidae), for the Miocene to modern species; here only Hominidae is recognized, with the human line classified as hominines (the subfamily Homininae). Thus *Dryopithecus* (sometimes divided into the genera *Proconsul*, *Rangwapithecus*, and others) is the oldest recognized hominid, known in eastern Africa between about 23 and

at least 14 MY ago. Two species are also known from western Europe between 15 and 11 MY ago. As is usual in fossil primates (and other mammals), *Dryopithecus* is known especially by partial dentitions, supplemented by rare cranial parts and often unassociated limb bones (which are thus difficult to allocate to species defined from teeth).

The dentition of *Dryopithecus* is quite similar to that of modern apes, with a relatively thin coating of enamel on the molar teeth, although the incisors are not as large (compared to molars) as in living forms. The mandibular corpora of both *Dryopithecus* and modern great apes are similar in being relatively thin and deep, thus not adapted to withstanding heavy chewing stresses, and the two groups reveal similar proportions between molar tooth size and body size as estimated from limb bone size. Taken together, these features suggest an adaptation to eating foods which were neither tough nor gritty, perhaps forest fruits rather than savannah roots or tubers. This matches well with the known diet of living great apes as well as with the evidence from the fossils themselves: African *Dryopithecus* especially had a rather monkeylike limb structure, rather than any special adaptation to terrestrial life, and the paleoenvironments appear to have been most like modern montane rainforests.

Africa was an island continent for most of the middle (and early?) Cenozoic, with a fauna distinct from that of Eurasia in general, but about 18 MY ago, northeastern Africa contacted Eurasia as a result of tectonic movement (continental drift), and the faunas of the two regions began to mingle. *Dryopithecus* species only slightly different from those found in eastern Africa probably reached western Europe by expanding along the northern shore of the Mediterranean and then northward into France and Germany, a route followed by other forest-dwelling animals of this time period as well. But a second group of more advanced apes, which can be called the sivapiths, also made its first appearance about 15 MY ago.

The sivapiths, or ground apes, as they have been termed by E. L. Simons and others, are important because they show the first clear evidence of anatomical features later found only in the close relatives or ancestors of modern humans. Several of these derived characteristics imply a greater adaptation to eating tough or gritty foods, such as might be found on the ground in a forest-fringe or savannahlike environment. They include: thicker enamel on the occlusal (chewing) surface of the molars and premolars, thicker and more heavily buttressed jaws (mandibular corpus and symphysis, maxillary alveolar processes), and apparently larger teeth relative to limb bone size, all by comparison to *Dryopithecus* (and modern apes). The limbs themselves are not well known, but there is not as clear evidence for terrestriality as was once thought (and implied by the name ground apes). There are three main varieties of sivapiths, here recognized as genera: *Sivapithecus*, *Ramapithecus*, and *Gigantopithecus*. Two of these appeared about 14-15 MY ago in Turkey, East Africa, and Czechoslovakia, then continued until approximately 8 MY; *Gigantopithecus* is only known in southern Asia around 9 MY and in southern China

around 1 MY ago. Although authorities differ on the allocation and interpretation of the fragmentary remains of the sivapiths, it seems that *Sivapithecus* is the most conservative form, with incisors and canines unreduced from the *Dryopithecus* condition and relatively monkeylike limb joints. The four recognized species compare in size with modern chimpanzees and gorillas. *Gigantopithecus* is somewhat larger and more robust, with gorilla-sized teeth in massive jaws. It appears more advanced morphologically, with one elbow fragment showing gorillalike adaptations, perhaps to ground life. The front teeth are all reduced, but the canines, although low-crowned and not strongly sharpened by their opponents, are thick and were used as additional food-grinding surfaces. *Ramapithecus*, the smallest and most poorly known of the sivapiths, may be the one most similar to later humans. It has especially thick and shallow mandibular corpora, its incisors and canines appear to be small, and the canine may be rotated slightly to align more with the incisors. In addition, the ultrastructure of the enamel prisms shows the so-called keyhole pattern. All of these features, in addition to those noted above for all sivapiths, are found in Pliocene *Australopithecus*, although some of them may be reduced in Pleistocene *Homo*.

New finds. Most of the sivapith species were first recognized by 1930, but only recently has their importance become clear. This new understanding is due mainly to the recovery of many new specimens, especially in the Potwar Plateau ("western Siwaliks") of Pakistan. There, D. R. Pilbeam directed a team which carefully investigated the many thousand feet of fossiliferous sediments. Rather than relying mainly on specimens brought in by local villagers, Pilbeam's crew collected intensively in small areas, so that each fossil could be carefully tied into the rock sequence, some of which can now be dated by geophysical means. The new fossils have often been more complete than those found earlier in this classic area, and in 1980 a real prize was recovered: a partial face and nearly complete lower jaw of *Sivapithecus*, now being reconstructed for study. A team from the Peking Institute of Vertebrate Paleontology and Paleoanthropology discovered contemporaneous fossils in a new site in Lu-feng County, Yunnan Province (southwestern China). So far, this locality has yielded two nearly complete mandibles, over 200 teeth, and a crushed partial skull, probably also of *Sivapithecus*. Comparable specimens, including a palate and a fine series of mandibles revealing strong sexual dimorphism, have been recovered from a single locality in northern Greece, and less complete groups of specimens have come from Turkey, Hungary, Kenya, and of course the classic Indian Siwaliks. New studies of the paleoenvironments of some of these localities have generally produced a picture of open woodland landscapes, the interface between forest and steepe/savannah, including fluctuating ecotonal microhabitats. In such areas, it would appear that the human lineage became evolutionarily distinct.

Several implications arise from this interpretation of the middle and late Miocene hominoids. First, the presence in the sivapiths of derived (advanced) features found only in humans among

modern hominoids strongly suggests that they fall on the human side of the ape-human divergence, thus dating that divergence as older than 15 MY. Studies of the proteins of living hominoids have shown that humans are more similar to chimps and gorillas than any of these are to orangutans. Thus, the Asian-African ape divergence was probably even older. On the other hand, some preliminary studies suggest resemblances between orangs and *Sivapithecus* in details of enamel ultrastructure and thickness; along with their geographical proximity, this has led some authors to postulate an ancestor-descendant relationship between the two genera. This ties in closely with a more contested aspect of the protein studies, their use as a "molecular clock" to date the time of divergence of the groups studied. Without considering the theoretical controversy over such clocks, the molecular results have suggested an ape-human divergence date of less than 8 MY, far too recent in light of the fossil evidence. Some paleontologists, including Pilbeam, have suggested that the sivapiths might include the ancestors of both great apes and humans, but their derived traits shared with *Australopithecus* make this view untenable to others, including the present writer. It is, of course, possible that these features were evolved in parallel by the sivapiths and the later hominines (*Australopithecus* and *Homo*), but this is unparsimonious and thus to be rejected as the hypothesis of choice unless simpler theories are falsified. In fact, the morphology of the earliest *Australopithecus* is more similar to that of the sivapiths than to living or earlier apes, as might be expected if the two groups were genealogically related.

Many problems concerning the sivapiths remain to be solved, from their formal names to their area and time of origin. For example, the group has been recently called or placed into Hominidae, Hominae, Dryopithecinae, Dryopithecidae, Sivapithecidae, Ramapithecidae, Ponginae, and Sugrivapithecini, among other taxonomic units. Some authors recognize only two genera, combining *Ramapithecus* into *Sivapithecus*, while others accept seven or more, plus other early Miocene African genera here called *Dryopithecus*. East Africa, Arabia, Turkey, central Asia, and other areas have been suggested as the locale of their origin from a *Dryopithecus*-like stock, and numerous theories have been put forward to account for their appearance. More detailed analyses of their functional morphology, taxonomy, and habitat, involving new fossils and comparisons with close relatives, may help to solve these problems, at least temporarily, but they will doubtless raise others to keep paleoanthropologists busy with ancestors of modern humans.

[ERIC DELSON]

For background information see FOSSIL MAN: PRIMATES in the McGraw-Hill Encyclopedia of Science and Technology.

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Note: the bibliography above also includes references for *Human Culture* by D. P. Gifford.