throughout the life-span of an individual. "What mechanisms . . . could account for such a progression? What kind of 'shifting' organ are we dealing with? . . . 'Decrease of plasticity' with age is a description of the phenomenon, not an explanation of the data," they argue. "[T]he anatomical integrity of functional units seems an irrelevant consideration."

Not everyone who sympathizes with the linguist's view of the brain agrees with Morton and Marshall about the irrelevance of neuroanatomy. "Structures that are revealed once they've become neurologically fixed won't necessarily identify what the original components of a skill were," says psycholinguist Thomas Bever of Columbia University, but structural studies "can tell us something of the capacity itself. I don't claim that components of the [language] module will be . . . particular pieces of neurological 'real estate'—[but] one intent is to create a theoretical psychology that will tell us where to go looking anatomically."

Marshall and Morton seem willing to concede that the learning behavior of simple organisms can be understood according to such rules: "[T]he relationship between learning theory and natural behavior is only to be determined through functional representations of what the organism's nervous system does, not what it is. With simple organisms, such as *Aplysia*, this relationship can most readily be established in terms of its neurophysiology and neurochemistry."

But beyond such concessions, they are not yet willing to move. "With humans it can at best only be done abstractly," they continue. "Thus, suppose it turned out that all human synapses were equivalent to *Aplysia*'s, and suppose that all the behavior of such a synapse were expressible in terms of learning theory. Suppose further that we had all the human neurobiological information there was to have. We might then have an account of natural human behavior and that account might be couchable in learning theoretic terms, but we would not have an explanation in terms of the questions we really wanted to ask."

—**Jeffrey L. Fox**

Is the Orangutan a Living Fossil?

Molecular biology and paleontology have combined recently to arrive at a consensus on human/ape evolution; a new Kenyan fossil stirs the debate once more

Earlier this year Richard Leakey, of the National Museums of Kenya, in company with Alan Walker of Johns Hopkins University, found upper and lower jaw fragments of an extinct ape about the size of a male chimpanzee that lived in northern Kenya about 17 million years ago. The discovery, made public at the beginning of December, adds a new and somewhat controversial element to the emerging view of human and ape origins over the past 20 million years. For instance, proffers Walker, it might be provocative to consider the orangutan as something of a living fossil.

For a long time there has been a general assumption that the orangutan, which lives in Asia, is evolutionarily the most specialized of the great apes, whereas the African great apes (the chimpanzee and gorilla) are more primitive and therefore resemble more closely the last common ancestor between apes and humans. "These fossils raise the interesting possibility that it might be the other way around," suggests Walker.

In addition to their evolutionary implication for modern great apes, the fossils may have an important bearing on estimating the time of divergence between the human line (hominids) and the African apes. This has long been a matter of much dispute but was until recently considered by most paleoanthropologists to be about 15 million years. Results from studies of proteins and DNA have for some time been taken by certain molecular biologists to imply a divergence date of 4 or 5 million years, a relatively recent split but one that paleoanthropologists have now begun to take seriously. The great age of the new Kenyan fossils, with their apparent affinity with the modern orangutan, might once again push back that all important date, to around 10 million years.

The modern apes are but a remnant of a once widespread and diverse group. The ape lineage appears to have arisen almost 30 million years ago and began to flourish in the tropical forests of Afro-Arabia. Although the fossil record of the Miocene epoch (25 to 5.5 million years ago) is at best spotty, it is clear that by 20 million years ago there were at least six species of the genus *Proconsul,* which group is considered a good bet as being ancestral to the living apes and hominids. Around 17 million years ago tectonic plate movement brought Afro-Arabia into contact with Eurasia, whereupon a great interchange of faunas occurred between the two landmasses. Apes took part in this interchange and proliferated greatly throughout southern Eurasia at a time when cooling global climates reduced much dense tropical forest to more open woodland.

Included in the great Miocene diversity of apes in Africa and Eurasia were two of especial interest: a small creature, named *Ramapithecus,* which for a long period was considered the best candidate as the first hominid; and a larger version, named *Sivapithecus*. Until recently, both these forms were known primarily from specimens of jaws and teeth.

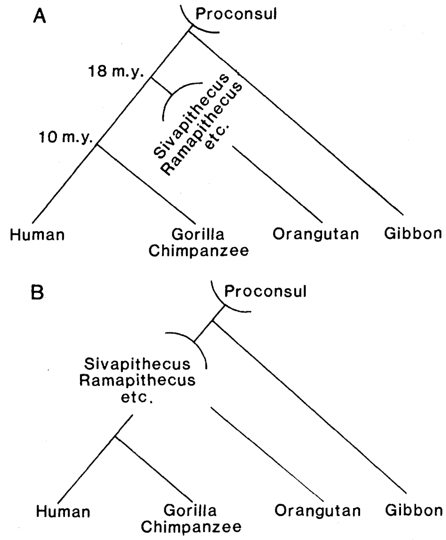
The anatomical features that gave *Ramapithecus* its designation as probably the first hominid were its robust jaw and thick layer of enamel that capped its cheek teeth. *Ramapithecus* shares these with the later undoubted hominids, the australopithecines, the oldest known fossils of which date to almost 4 million years. Because there has always been a tendency to view hominid features as specialized and those of apes not, the robust jaw and thick enameled teeth of australopithecines were so classified. *Ramapithecus,* endowed with these same characteristics, was therefore also thought to be specialized and, because of its inferred small body size, was generally designated as the beginning of the human line. The age of known *Ramapithecus* fossils, which range from 8 million to 14 million years, provided the probable divergence time between hominids and the apes: 15 million years.

Modern human molar teeth have relatively thick enamel, which continues this supposed diagnostic trait. Chimpanzee and gorilla tooth enamel, by contrast, is thin. This appears to fit the inferred evolutionary pattern, with the great apes supposedly representing the primitive condition. Orangutans, however, disrupt the pattern: they have relatively thick enamel, an inconvenient fact that has frequently been ignored.

The tendency to characterize all hominid features as specialized, or derived, was part of a mind-set that lumped all ape origins together and distanced them from those of hominids. The work on proteins, which began in the 1960's, and subsequently the DNA studies, has shattered this comfortable concept. It is now clear that the evolution of humans and apes, known collectively as hominoids, involved first the divergence of the gibbons, followed by the orangutans, followed by a split between hominids, chimpanzees, and gorillas. The order of this last event—the hominid/chimpanzee/gorilla divergence—is still unclear. What is clear, however, is that the African apes are more closely related to humans than either is to the Asian great ape, the orangutan.

The molecular work not only provided a branching order of hominoid evolution but also put a time on each event, a time generated by the so-called molecular clock. Allan Wilson and Vincent Sarich, biochemists at the University of California, Berkeley, have been championing the clock, and with their version get dates of 12 million years for the gibbon divergence, 10 million for the orangutan, and 4.5 million for the hominid/African ape split. The nature, accuracy, and relevance of the Wilson/Sarich clock has been repeatedly challenged. Other molecular biologists using different techniques, such as Charles Sibley at Yale University who measures the passage of time in differences in whole DNA hybridization, generally get earlier divergence times. Sibley's for the hominid/African ape divergence, for instance, is between 7 and 10 million years.

Although the differences among proponents of the various molecular techniques have yet to be reconciled, even the oldest dates from any of the clocks give no comfort to the traditional date of 15 million years for the hominid/African ape split. This threw *Ramapithecus* and its fellows into an uncertain status, a limbo from which they were rescued by the discovery in 1980 of a beautifully preserved *Sivapithecus* face from Pakistan. When David Pilbeam of Harvard University, but then at Yale, described the specimen in January 1982 he noted features of the premaxillary region, the palate and the eye orbits that, he said, aligned the fossil with the modern orangutan. Peter Andrews of the Natural History Museum, London, was coming to the same conclusion on different specimens.



Hominoid evolution: two possibilities

(A) *If the facial features of* Sivapithecus *and* Ramapithecus *are specialized characters shared with the modern orangutan, the group is not ancestral to the later apes and hominids. The dates of the divergences would then be as shown.* (B) *If the* Sivapithecus/*orangutan face is primitive, then the group could be the common ancestor to the later hominoids.*

By associating *Sivapithecus* with the orangutan in this way, several things happen. First, the orangutan gets itself an ancestor, which is a rare thing among modern apes. Second, as *Ramapithecus* shares so many features with *Sivapithecus,* it must be placed in the same group, or clade: so, in fact, there is an orangutan clade, not a single ancestral species to the modern ape. And third, as the Pakistan specimen is so firmly dated, at 8 million years, there emerges a minimum date for the orang divergence. In fact, when Pilbeam described the new Pakistan specimen there were others from the same and other localities that could be dated to around 13 million years. On this basis Pilbeam inferred a hominid/African ape split of between 7 and 10 million years. All this derived from the finely preserved facial features.

Here, then, was a neat picture emerging. But, as Pilbeam cautions, "The Miocene record is still sufficiently sparse for reasonable people to hold firmly quite different opinions." And so it was to be, when the newest fossils came out of Kenya this year.

The fossils include the front section of the lower jaw and part of the upper jaw with some attached facial structures. According to Walker the lower jaw matches very clearly the pattern seen in the Pakistan *Sivapithecus* fossils. Although the facial structure is much less complete in the Kenyan fossil, Walker says that from what can be discerned he would again match it with the Pakistan *Sivapithecus,* though, very reasonably, neither he nor Leakey have designated a species name. Pilbeam, who so far has seen only casts of the fossil only very cursorily, is less sure it is the same as the Pakistan fossils and thinks it might be a different genus.

If the new Kenyan fossil is indeed a *Sivapithecus,* and if, as Pilbeam believes, the *Sivapithecus* features indicate that the clade has already specialized away from the hominoid stock, then the ancestry of the orangutan is taken back to at least 17 or 18 million years. By association, this drags back the date of divergence between hominids and the African apes to at least 10 million years, which is contentious enough. Walker's second suggestion for the interpretation of the new material is even more so.

Sivapithecus is an interesting mix of traits as seen from the cranial material. The robust jaw and teeth structure appears to represent a primitive morphology and goes through to the hominids. The African great apes specialize away from this. The difficulty in interpretation comes with the face. Pilbeam believes that these features are specialized to the clade and he says it is difficult to see how they could be ancestral to the later hominid and African great ape anatomies. In other words, the facial features, in their fully developed form, are specifically associated with the Asian line.

Reasonable man that he is, Walker disagrees. He argues that one cannot dismiss the possibility that the facial features are primitive; that is, they could be a characteristic of the basic hominoid stock of the time, the common ancestor. Unfortunately, the new Kenyan specimen is not complete enough to determine how fully developed these facial features were 17 million years ago. If these features are primitive and the equivalent structures in the australopithecine, chimpanzee, and gorilla can be derived from them, then, as Walker suggests, the orangutan is not a specialized ape at all but instead is something of an echo of the evolutionary past, a living fossil. And the chimpanzee and gorilla are not primitive species that give us a glimpse of the last common ancestor but rather are specialized apes instead.

The question rests upon the facial features: are they primitive or derived? There is no certain way to decide as yet, but more fossils would help.

Walker mentions a third possibility for the new Kenyan fossils: that they merely represent one of the many Miocene apes, now extinct, that had little to do with anything later. "But," observes Walker, "you can say that kind of thing about any fossil, can't you."—**Roger Lewin**