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Watching the film *Inherit the Wind* recently, I was struck by the scene showing the carnival atmosphere in the town where the. movie rendition of the Scopes trial was about to take place. There is a musical background of *Give Me That Old Time Religion*, and a visual background of waving placards and drawings to the. effect that man did *not* evolve from the apes, and then, as the height of ridicule, a carnival exhibit features a cigarette-smoking chimpanzee sitting under a sign that offers the message, "Darwin was wrong – the apes evolved from man!" Now, two full generations or some six decades after the trial and long after the film was made, I have come to wonder how ridiculous this message actually is? Not the first one, but the second.

In part, this probing of what on the surface seems to be a senseless statement, in a movie scene meant to show a spoof of science, is a direct consequence of a vastly increased scientific knowledge about the past. Simply put, we see things more clearly than we did sixty years ago, although I must admit that this vision is still, by any standard, very blurred at best.

To feel what it is like to view into the past with the frustrations of a prehistorian, imagine setting up two good mirrors to face each other. If you step between them, positioning yourself just right, you can see yourself in the first mirror just as you stand before it. You will also see a second smaller image of yourself reflected from the second mirror into the first mirror, and an even smaller image reflected from the first mirror to the second and then back to the first, and so on. It's a big "so on," in fact, because in a theoretical sense the number of decreasing images should be infinite. But mirrors are not perfect, and you probably did not line them up exactly right, so at some point you stop seeing any smaller images. As long as you are imagining, also imagine that a close examination of the images shows that the first, biggest one looks (perhaps surprisingly) slightly different from you. The next smaller one is more different, and the next smaller one is more different yet. Just when the differences accumulate enough to make the images interesting, they are so small that you can't see them clearly any more.

With a focus problem like this, it is a wonder that any progress is made at all. In fact, what progress there is in understanding human evolution could never result from this tunnel view into the past alone. Theory, and in particular the process of testing explanatory hypotheses, must become involved.

Years ago Karl Popper made the claim that history is not and cannot be a science. He seemed to extend this claim to the so-called historical sciences (geology, paleontology, prehistory), although recently he made it clear that he regarded the study of biological evolution as science. Many of us believe that what makes evolutionary studies science is the testing of hypotheses about past events. It is in this process of testing, and in particular in the attempts to refute hypotheses, that the scientific nature of prehistory lies. It is here that the relation of theory and fact can best be seen in general, and in the specific issue of human (or ape) descent.

Curiously, also involved in this probing is an issue of taxonomy, the theory and practice of classifying organisms. In fact, the problem I raise might best be considered an issue of philosophy because it involves the most fundamental questioning of humanity's place in nature. Taxonomy is usually a bore to write about, if not to think about. The philosophy and "art" of classification may well be critical to museum curators, who after all do need to know what

specimens go on the shelves together and what labels should be put on them. For the rest of us, however, it seems to be the last holdout for the arcane reckoning of how many taxa indeed can dance on the head of a pin. Taxonomy is supposed to reflect evolutionary history, just as terms of human kinship (father, cousin) reflect genealogy. But like any spinoff of scientific thinking (evolutionary history is, after all, a scientific hypothesis about what someone thinks happened in the past), taxonomy probably reflects the taxonomists at least as well as it reflects the taxonomized. And when the object of taxonomic focus is humanity, it becomes a formal statement of "them versus us," always to the benefit of us, and to the detriment of them. Perhaps it truly doesn't matter, at least as long as none of the other species involved can talk back, but standard operating procedures in prehistory have recently created a mess – a real intellectual tar baby that has stuck to everyone who has come near it.

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The story can start with "man and the apes," an unfortunate phrase that is not only sexist but now appears to be overly anthropocentric as well. The great apes have long been the evolutionary contrast to humans. These large primates, the gorilla and chimpanzee of Africa and the orangutan of southeast Asia, are commonly taken to represent human ancestors; after all, "man descended from the apes" (if not from the trees!). We are the featherless bipeds, with the large brains set above hairless bodies. They, in contrast, are the hairy, smelly (been to a zoo lately?), long-armed tree dwellers of Tarzan fame. Apes are the "them" who almost became "us," but never fully made the grade. The taxonomists gave us the perfect handles to put on these thoughts: the hominids and the pongids (or if you like the Latin, hominidae and pongidae) ..The hominids are the humans and all of our ancestors back to the split with apes, and the pongids are the apes and all of their ancestors back to the split with humans. Thus we are formally set apart from them – and why not? Aren't we *really* different?

Everyone knows there is a gap between humanity and the apes, *u* series of consistent differences that helps outline our humanity. Some of these differences are unique to us — bipedalism (upright, two-legged locomotion); large brains and associated behaviors that are very complex (social behavior, language, stratified roles, etc.); weak and relatively hairless bodies that must rely on technology; cunning, and skill to survive and persist; and so on. Others of these differences are communalities uniquely shared by the apes. These include similarities of habitat (dense tropical forest), and of size and form (for instance very elongated forelimbs relative to the hindlimbs), a strange mix of arboreal life (involving climbing, hanging and a limited amount of brachiation), and a terrestrial adaptation that shows these same primates to be capable of both bipedal walking and walking on all four limbs (with the knuckles or fists rather than the palms of the forelimbs on the ground). If it is the contribution of taxonomy to state these facts in a formal way, it's fair to ask what's wrong with that?

Well, the taxonomic contrast of hominids and pongid is a contrast that we call sister groups. This means exactly what it sounds like, sister groups are so close together in their relationship that they share an immediate common parentage. You and your brother are sister groups, showing if nothing else that the term is not meant to be sexist! But assuming that you still have the brother you just had above, you and your cousin are *not* sister groups because your brother shares a more recent parentage with you than your cousin does.

That the common parent of "man and ape" was neither a man nor an ape has been realized for a long time, although the popular accounts still have us descending from apes. However, that is not the problem. The problem comes from the last decade's research that shows that hominids and pongids are not sister groups – humans are not the sister group of apes!

A good deal of this research is paleontological. In particular, it hinges on a fossil primate

called *Ramapithecus* – a primate once thought to be a unique human ancestor. The relationship of *Ramapithecus* to the human line is not only important in establishing the interpretation of *Ramapithecus*, it has also turned out to be critical in our understanding of the positioning of the human line itself.

When its fragmentary remains were first discovered in the Siwalik hills of India, just a few years after the Scopes trial took place, the initial interpretation of Ramapithecus was dictated by Darwin's ideas about human origins. The Darwinian theory of human origins was and has remained very powerful, and in one way or another it has influenced virtually every attempt to hypothesize about how humans arose and evolved. Darwin proposed that there was a positive feedback relation between the four elements he viewed as distinguishing humans from the apes: bipedal locomotion, tool use, reduction of the canine teeth, and expansion of the brain. He hypothesized that there was a fundamental shift in adaptation that occurred when humans first appeared; he believed, in fact, that this shift *caused* the appearance of the human line to take place. Darwin contended that the ancestors of the human line, as well as of the ape line, had a very ape-like arboreal adaptation, involving dietary, locomotor, and behavioral factors. The human line separated from the ape line, originating as a distinct entity because this adaptation changed to a terrestrial one and a primarily frugivorous diet was replaced by one emphasizing meat obtained by hunting in the population of primates that were the earliest human ancestors. Tool use attained importance, because tools were used in hunting and for defense. Bipedalism appeared as a means for freeing the hands during locomotion to hold hunting weapons and carry them freely. The canine teeth diminished in size because tools replaced their cutting, slashing, and threat gesture functions. Lastly, expanding brain size resulted from the evolution of human culture – a complex of social and technological behaviors that may have first gained importance as a means of insuring that the proper and appropriate manufacture and use of tools is accurately transmitted from generation to generation.

When the first fossilized bones and teeth of *Ramapithecus* were found, they were thought to be the remains of a hominid because they fit the Darwinian model of human origins. Even though these fossils were very fragmentary, consisting of an upper jaw with some teeth in it, the socket for the canine tooth seemed to be small and in general the shape of the incomplete toothrow was interpreted to be human-like. Thus, from the time of its first discovery, *Rarnapithecus* was inserted onto the human line, at its very beginning. As more remains were slowly recovered, attempts were made to show how they fit this Darwinian model, even to the extent that a search began for evidence of the stone tools that these earliest hominids "must have" been making. This search was successful! Similarly, long before any limb bones of *Ramapithecus* were found, it was proclaimed to be a biped. In sum, such is the power of theory that the fragmentary remains recovered for *Ramapithecus* during the years between 1960 and 1975 were "known" to be those of the earliest hominid because they fit Darwin's theory of hominid origins, while Darwin's theory was known to be correct because the fossil evidence (i.e. the fossilized jaws and teeth of *Ramapithecus*) fit it.

The trouble came when more complete remains of *Ramapithecus* were found. These remains showed that the earlier interpretations were mistaken. The canines were not particularly small when body size and the normal differences between male and female canine teeth were taken into account, and moreover the canines were used just as modern ape canines, for cutting, slashing, and threat gestures. The discovery of limb bones showed the creature was not at all bipedal, and it was found to have a rather small brain size. The evidence for stone tools associated with *Ramapithecus* was never very convincing and with the more complete discoveries this assertion too was debunked and dismissed. Yet, interestingly, just as *Ramapithecus* was losing its position as the earliest hominid because it was no longer seen to fit Darwin's model of hominid

origins, Darwin's model itself was being replaced.

At the beginning of the last decade, a (then) young man named Clifford Jolly proposed that Darwin was wrong in his thinking about human origins, and that the real explanation of what happened lay in a very different sort of shift in diet. Jolly's ideas were based on his studies of baboons. During the course of his studies he found that one particular type of baboon, the gelada (a form that today lives mostly in the dry grassy highlands of Ethiopia), had a number of features and behaviors that were very much hominid-like, and especially similar to the features found in the remains of the earliest upright hominids, the australopithecines. Because the geladas are not very closely related to humans, and since they are obviously not ancestral to humans, Jolly reasoned that the parallel similarities between these features stemmed from similarities in adaptation. Thus he used the living geladas as a model for some aspects of what early hominids must have been like. He called his hypothesis the "seed eaters" model of human origins because he believed that the adaptations involved in eating small hard seeds found on the African grasslands were the cause of the parallelisms between the hominids of millions of years ago and the geladas of today. While Darwin posited that early hominids evolved to take advantage of the African grasslands by hunting the game that lived there, Jolly contended that the hominids evolved to take advantage of this rich environment by adapting to eat the abundant seeds that grew there.

Jolly's model linked together canine reduction, upright posture and bipedal locomotion, the development of the opposable thumb, the appearance of language, and the evolution of a powerful chew- ing apparatus (involving the jaws and teeth and the muscles that operate them) adapted for a diet requiring day-long grinding and crushing of seeds. Jolly did not deal with brain size because by the time he had developed his model it was clear that the earliest hominids did not have brains that were any larger than the brains of living apes. Brain size, in other words, attained its unusual magnitude *after* hominids originated. In fact, brain size has increased all throughout human evolution, suggesting that intelligence and behavioral complexity have been improving from the very beginnings of humanity. However, according to Jolly's model, neither culture nor tool use played an important role in these beginnings.

The seed eaters hypothesis received a good deal of support from prehistorians because, as mentioned above, though *Ramapithecus* did not fit Darwin's model very well, it was an excellent fit for Jolly's. Attention shifted from the front to the rear of the toothrow. *Ramapithecus* became known as a primate with very large jaws and molar teeth and a specific adaptation for long periods of powerful chewing dietary items such as seeds whose digestion requires a good deal of grinding and crushing in the mouth. Moreover, these very features also had been found in the earliest upright hominids, the australopithecines. The jaw of the famous little lady Lucy, for instance, was seen to be virtually identical to a number of *Ramapithecus* jaws. Thus, *Ramapithecus* seemed to be saved by the belle.

However, another problem soon appeared. By the end of the 1970s, the fossil remains of several complete *Ramapithecus* heads were discovered. These came from sites as far apart as Hungary, south China and Pakistan. They agreed in revealing that contra to all expectation, *Ramapithecus* showed extraordinary similarities to one of the living great apes, the orangutan. These similarities were specific and were not shared by *Ramapithecus* and the other great apes, or by *Ramapithecus* and humans. Thus, it has become evident that the Asian *Aamapithecus* form is an orangutan ancestor.

Then, an African *Ramapithecus* form was discovered at a Kenyan site called Buluk where the remains are double the age of the Asian species. These remains, and the early date attributed

to them, showed how truly mistaken the original interpretation of *Ramapithecus* actually was. Instead of being a hominid, the unique father of us and only an uncle to the apes, one species of Asian *Ramapithecus* turns out to be the unique father to the orangutan while the much older African *Ramapithecus* species is *everybody's* grandfather.

There is one more related problem, which comes from the hominid/pongid dichotomy discussed above. This commonly accepted taxonomic contrast reflects what everybody "knows": there are humans on the one hand, and there are apes on the other (us and them). Formally, genealogically, or taxonomically, this would make humans the sister group of chimpanzees, gorillas, *and* orangutans. However, this is not the case. Instead, the fact is that the orangutan is the sister group for all three living African hominoids: gorillas, chimpanzees, and humans.

Evidence for this relationship is based on genetic comparisons. At first, several decades ago, these were determined from the study of proteins. Until very recently, it was just too hard to discover many of the specific details on the DNA molecules themselves. However, proteins are the direct products of the genes, the information stored on the DNA molecules. The molecular structure of proteins there- fore reflects the exact sequence of information stored on this molecule of heredity. In theory, then, the structure of the DNA in different animals could be compared by studying the exact structure of the proteins. In fact, this did not prove to be particularly easy. At first it was only possible to ascertain gross protein similarities. This was done by calibrating the reaction of a species' immunological system to the proteins from other species. Later it became possible to study the proteins directly. By exactly determining the detailed protein structures, and comparing the protein structures for different species, it appeared possible to determine the sequence of divergence for the species compared; that is, which two species separated first, which separated next, and so on. Most recently, it has become possible, if not commonplace, to directly compare DNA structures them- selves (i.e., the exact progression of base pairs on the DNA molecule) to ascertain the sequence of divergence. As a consequence, for a group of species one can now determine which two species diverged most recently (i.e., which two have the most recent common ancestor – like sharing a parent), which third species this sister group of two species diverged from most recently (like sharing a grandparent), and so on. For humans the sister species is almost certainly the chimpanzees. For the sister group of humans and chimpanzees the closest relative is the other African hominoid (the category that includes humans and apes) – gorillas. Finally, the large Asian ape, the orangutan, is a sister group to all three of the African hominoids considered together.

Thus, the genetic evidence shows that among the hominoids the orangutan diverged from the African line first. Then later the gorilla diverged from the chimpanzee/human line, and finally most recently the chimpanzees and humans diverged from each other. How recent was this last divergence (the divergence referred to as "human origins")? Four to 7 million years ago is a reasonable estimate, and my opinion is that it is not likely to be much longer ago than 5 million years.

The paleontological evidence shows that the very first divergence, between the Asian and the African lines, was a division of *Ramapithecus* species. The Asian branch went on to eventually evolve into orangutans. This branch retained many of the ancestral features, and *Ramapithecus* remained a valid and useful name throughout much of its evolution (remember, the name was first applied to the Asian branch). The African branch also retained many of their original features. These were present in a younger species (called "Kenyapithecus" after its country of discovery) that was still old enough to be the common ancestor of African apes and humans, and as Jolly noted these original features remained common in the African hominoids

and continued on to characterize the earliest bipedal hominids. It was the African apes that came first to notably and dramatically diverge from this adaptive complex.

In taxonomy, groups classified together should each be like families lining up for their Christmas pictures – nobody is supposed to be left out. If someone *is* left out the group is no longer monophyletic; that is, it no longer consists of a group of ancestors (parents, grand-parents, or whatever) and *all* of their descendants. Leaving a few of the family's bad sheep out may make for a better picture, but taxonomists don't like it because the group is no longer a natural one. In talking about the human family, it is easy to make up a monophyletic group of the living. Simply include all living humans. So much for the us, but what about the them, the apes?

If we think about the apes as a family (or as one of the classes in a taxonomy), the requirement that nobody in the family can be left out *means that humans must be left in!* Otherwise it would be like taking a picture of your family with your brothers and sisters, parents and grandparents, aunts and uncles., and all your cousins, but without you. The indignant feelings you would have in sending out a Christmas picture like this should be matched by equally indignant feelings should someone refer to the apes *as a taxonomic group* leaving us humans out.

This doesn't do much for the "us versus them" attitude we have about the apes, but it might help stimulate efforts in conserving apes in their natural habitats, before it is too late. More importantly, perhaps in this changing perspective of who has to be included in the Christmas picture there is some insight to be gained about ourselves. Phrases like "the naked ape" were once coined because of the descent-from-the-apes perception of human evolution, and widely rejected because the perception was incorrect. Descent-from-the-apes was wrong because it was the wrong way of looking at our relation to the apes. The fact is that in terms of genealogical relationships we are apes, albeit of a very special kind.

What makes us special is the use we have made of culture as our adaptation, the ways we have learned to deal with the world, and *not* our relationships with other primates. The fact is that our origins did not make us what we are, and it is not our genealogy that makes us unique. Our beginnings sent us down a path that has led to an extraordinary success. If there is something for our species to learn about itself from our blurred prehistory, it is perhaps to be found in the steps we have taken and continue to take down this pathway, and not in where the path began.