

It was the summer of 1977, and the cause for all the hollering was a collection of hominid fossils recently uncovered in Hadar, Ethiopia. Donald Johanson, discoverer of the fossils and curator at the Cleveland Museum of Natural History where they were kept, was convinced (as was his deputy, William Kimbel) that there were at least two species of hominid represented in the collection. Tim White, an anthropologist at the University of California at Berkeley, saw only one. As Johanson recalls in Lucy, his book about the Hadar fossils, White ultimately won that argument. After an exhaustive analysis of the fossils and a comparison with the large collection of ape bones at the museum, Johanson and Kimbel would come full circle. "One thing," they both say today: a very primitive animal called Australopithecus afarensis, the original hominid, or ape-man.

Underlying the question of how many species existed in ancient Ethiopia is a much more fundamental question: how to draw the family tree explaining the transition from ape to human being. With Johanson and Kimbel convinced, there remained virtually no opposition to the single species point of view because, in 1977, very few scientists had seen the fossils. "Lucy," the 40-percent-complete skeleton that is the star of the Hadar fossil collection, had only recently been discovered and had yet to be named; and the new family tree — which put A. afarensis an-

## **Lucy's**Family Problems

cestral to both known hominids, *Homo* and *Australopithecus* — had not yet been published. But in the years since the discovery more and more anthropologists have had a chance to examine casts of Lucy and the other Hadar remains and to consider the evolutionary scenario, and the 1977 quibble is now being renewed. While the Cleveland-Berkeley camp is now yelling "one thing" in unison, others outside that group can be heard yelling back: "Two things."

The immediately apparent problem with the 3- to 3.4-million-year-old Hadar fossils is the extreme variation in size. Lucy was a diminutive adult, standing about three and one-half feet tall, with a slender, or "gracile," build. Other Hadar individuals - notably some of the socalled First Family, a group of 13 that apparently died together in some catastrophic accident — are relatively quite large, like smallish modern humans. Some scientists consider this in itself to be evidence for two species, but most do not; they point to such extant species as orang, which has tremendous sexual dimorphism.

Much more problematic than body size is the variation seen in morphology—both in the postcranial material (everything below the head) and in the cranial and dental remains. The Cleveland-Berkeley group — including C. Owen Lovejoy of Kent State University in Kent, Ohio, and Bruce Latimer of the Cleveland Museum—argues that the variation reflects differences due to sex and that such variation, though considerable, can be accommodated by one species.

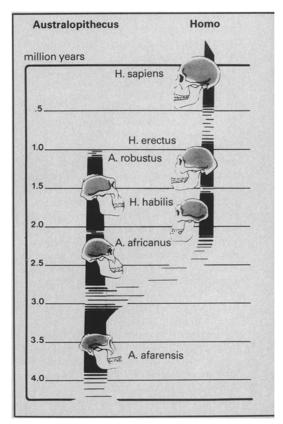
Others, to put it mildly, disagree. Indeed, the Cleveland-Berkeley group now finds itself in the position of defending its viewpoint against a growing number of critics—critics who, based on interpretations of nearly every bone in the body, would discard the one-species view and redraw the family tree. In the tradition of paleoanthropology, the debate is as acrimonious as it is confused, with the critics disagreeing even among themselves about what the bones say about human evolution.

The issue was raised in late April at a conference sponsored by the Berkeley-based Institute of Human Origins, which Johanson founded and directs. Two scien-

tists from the State University of New York at Stony Brook—anatomist Jack Stern and anthropologist Randall Susman — presented evidence, based on an analysis of the limb, finger, toe bones and pelvis, that the larger Hadar hominids had a different style of locomotion than did the smaller ones. The larger individuals were better adapted to bipedality, Stern and Susman said, while the smaller ones (including Lucy) were more arboreal: their fingers and toes show curvature which they interpret as an adaptation for grasping an arboreal substrate.

In the March American Journal of Physical Anthropology (where they published their results), Susman and Stern came down on the side of one species, a species characterized by "sexual dinicheism," where the females actually

Three competing views of early human evolution: say that Lucy and kin were actually unrelated, and would return to the once dominant view that A.



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New research on very old fossils has raised questions about one well-known family tree. Some scientists now believe that the bones and teeth of the oldest ape-men actually provide evidence for two distinct species—a finding that, if true, would push the search for a common ancestor back even further in time.

did spend more time in the trees and were therefore physically adapted for arboreality. Stern, at least, has since changed his mind. Based on further analysis of the variability in the curvature of the finger bones, he says that he is now leaning toward a two-species explanation. Although he says that the sample size is too small to be conclusive, he argues that the finger bones clearly sort themselves into two groups; one group has strongly curved fingers—exactly like African apes—and the other has less curved (but identically curved) fingers, halfway between gorillas and humans.

"The finger bones pushed me over the fence," Stern told SCIENCE News. "Taken in conjunction with the differences in the ankles and leg bones, I had to ask myself: Do you ever see such differences in living

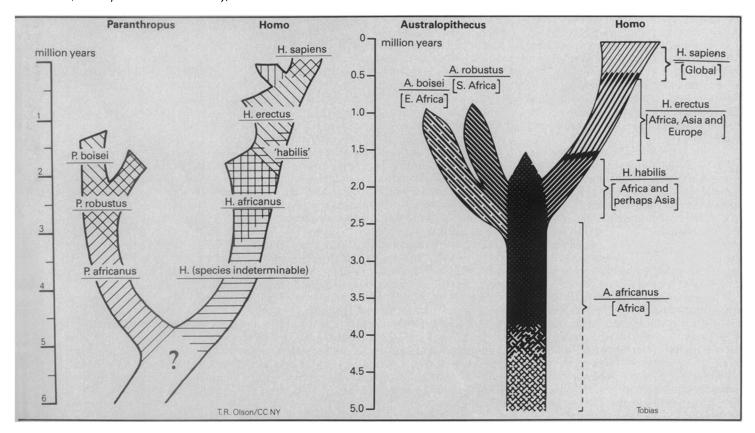
animals? And the answer is no—never. It's just too big a difference to be sexual dimorphism."

Stern's rethinking brings him into at least partial agreement with two French scientists, Christine Tardieu and Brigitte Senut of the University of Paris, who were the first to argue for two Hadar species based on postcranial evidence. Tardieu has reported differences in the shape of the femurs of the large and small specimens, and has argued that the differences indicate that some of the knees were better adapted for bipedal locomotion, suggesting that the two hominid lines split some time before; the larger individuals (the better bipeds) she calls Homo. Senut comes to the same taxonomic conclusion based on an analysis of the humerus, or upper arm bone; she has looked at sections of bone, which she claims reveal pronounced differences in a particular "fossa," or pit, and the ridge that attaches to the lower arm.

One indicator of the confusion in this debate is the fact that even those who argue for two species cannot agree on which of the Hadar hominids belongs in which species and which of those species is more closely related to *Homo*. The French divide the sample into a large and small species, but according to Stern's analysis they don't fall that way. And where the French place the larger, more bipedal individuals on the *Homo* line, Stern suggests that perhaps the arboreal Lucy-like animals, which were less evolved at the time, eventually led to the more successful human line.

The Cleveland-Berkeley group takes

Some scientists argue that A. afarensis, the species comprising "Lucy" and her kin, was ancestral to both major hominid lineages (left); others that the smaller Lucy eventually evolved into Homo while her robust neighbors were becoming extinct (center); and there are those, finally, who africanus (now expanded to include Lucy) is the ancestral stock.



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issue with both the Stony Brook and the Paris studies — but for different reasons and in markedly different tones. Of the Stern-Susman analysis, Latimer says that it doesn't make sense to interpret bone curvature in terms of function. Bones curve in response to the stress caused by many habitual behaviors, he says, and so it is not possible to conclude that curvature suggest arboreality. And bone curvature certainly should not be used in making taxonomic distinctions such as Stern is now doing, Latimer emphasizes. Stern and Susman disagree, pointing out that in all extant species arboreality is correlated with curvature of the toe bones. On this point they get support from University of Chicago anthropologist Russell Tuttle, who has also argued that the Hadar hominids were tree dwellers: "Latimer has got to come up with an alternative explanation for that curvature," he says.

Tardieu and Senut were invited but did not attend the Berkelev conference, reportedly because they do not like the intensity of American anthropological debate. And indeed, Johanson and White have been devastating in their critique of the French work, both at the conference and in recent interviews. White says the French evidence is "extraordinarily weak"; Johanson dismisses it as "sloppy science."

'Senut's evidence for Homo at Hadar rests on the most weathered, most fragmented distal humerus in the collection, Johanson says. "And some of the traits she sees, others of us simply cannot see." White also says that she has supported her conclusions with line drawings of the fossils that, when checked, don't match the fossils they are supposed to represent. And both argue that even if the French could prove that such variability exists that it is meaningless: such traits vary demonstrably in modern populations, they say, and more to the point they have no adaptive significance. And finally, Johanson says, "If there were two different taxa at Hadar, one would expect to see differences in the mandibles, teeth and skulls"

On this point almost everyone agrees; because all 3-million-year-old hominids were presumably walking upright at least some of the time, it is tricky to distinguish species on the basis of postcrania alone. Just as later species are distinguished by evolutionary specialization above the shoulders, so would two Hadar lineages (if they exist) be expected to show such cranial and dental adaptations. Some say they do; some say they don't.

Todd Olson, an anthropologist at the City College of New York, is challenging the integrity of A. afarensis on the basis of evidence from the skull and teeth in the Hadar sample. Suggesting a much different scenerio, he says that some of the individuals at Hadar show a particular characteristic in the mastoid region at the base of the skull; specifically, the mastoid of the larger specimens is "pneumatized," or in-

## The Ancestor-Dubbing Debate

he hue and cry over Donald Johanson's identification of his Lucy and other Hadar specimens as one unique species, A. afarensis, has taken on several different expressions. Some paleoanthropologists, for example, have argued that the Hadar specimens represent more than one species. But there are those such as Phillip V. Tobias of the University of Witwatersrand in Johannesburg, South Africa, who for years have insisted that Lucy and the related Hadar specimens can be accommodated by one species, but that they belong to the long-established A. africanus variety. In May, at the "In Search of Man" L.S.B. Leakey Foundation meeting in San Francisco, Tobias reported that a recent "spate of new discoveries" at an excavation site in South Africa has strengthened his case for A. africanus.

It was Tobias's mentor, Raymond Dart, professor emeritus at the University of Witwatersrand, who first introduced the term A. africanus to describe the fossil remains of an immature skull discov-

ered in 1924 in Taung, a dolomite-limestone cave in South Africa. While it literally means "southern ape of Africa," A. africanus labels a species with certain unapelike, protohuman traits. Since the discovery of the Taung baby, excavations at four other cave sites in South Africa have uncovered hundreds more specimens that fall into this same category.

have found very nearly canus species. 100 new specimens from

Sterkfontein in the last 5 to 6 years," Tobias reported, "and this has given us an even more secure basis than we previously had for comparison with hominid collections from Hadar." On the basis of this comparison, he said, "I do not believe that the differences that exist between Hadar and the Transvaal site are sufficient to justify Hadar as a different species."

For example, Tobias and associates have discovered several broad, upper

central incisors at Sterkfontein. "Yet broad, upper central incisors have been claimed by Johanson...to be diagnostic of their supposed new species, A. afarensis," he says. "This feature certainly does not distinguish between A. afarensis and the long-known species of A. africanus."

But Johanson's colleague Tim White, of the University of California at Berkeley, told SCIENCE NEWS that the diagnostic feature of A. afarensis is an incisor that is larger than A. africanus's relative to the back teeth. "In A. africanus, the incisors haven't changed too much, but the back teeth are relatively bigger," White says. "I could match incisors from Homo erectus with incisors from Homo sapiens," he explains. "Does that mean that H. erectus was the same species as ourselves? Of course not," White says, "but that's exactly the kind of reasoning Tobias is using."

Nonetheless, Tobias says he has compared a Sterkfontein sacrum to a Hadar sacrum, a hip bone to a hip bone,

> femur to femur, and "the differences are virtually indetectable." The small differences that do exist, he says, are all that might be expected as a result of geographical variability, for instance, within a species. After all. Tobias notes, the East African hominids were an equatorial or tropical group, while the Transvaal ones were subtropi-

As is the case with many anthropological controversies, the A. canus issue has implications for the presumed family tree. Specifically, Johanson and colleagues suggest that A. afarensis is the most

primitive ancestor of man and on a line that splits into two paths: one leads to A. africanus and ultimately to A. robustus, a species that becomes extinct; and another leads to H. habilis and ultimately to H. sapiens (modern man). Tobias and associates, though, believe that A. africanus was ancestral to both A. robustus and to H. habilis, which is on a separate line that ultimately leads to modern man. "This," Tobias says, "is the crux of the matter." - Linda Garmon



An A. africanus broad, upper Tobias's recent fossil central incisor - recently disfinds occurred at one of covered by Tobias at Sterkfonthese cave sites - Sterk- tein - compared with the cenfontein, in the Transvaal tralincisor on an upper jaw from afarensis versus A. afriprovince - where he has Hadar. The similarities Tobias directed an intensive, has found in such comparisons 48-weeks-a-year excava- have convinced him that Hadar tion since 1966. "We fossils belong to the A. afriflated with air bubbles, Olson says. Olson interprets this inflation as an early adaptation having to do with head posture, which led to the "robust" *Australopithecus* line and eventually to extinction. (Because of a dispute about the technical rules of nomenclature, Olson prefers to call the robust lineage *Paranthropus*.)

Further, Olson says, dental evidence at Hadar is the opposite of what one would expect in a single sexually dimorphic species, and therefore demonstrates that there was a second, more primitive species, made up of Lucy and the more gracile specimens. Lucy, he says, represents the earliest appearance of Homo. Thirdly and finally, he argues that because the robust cranial adaptation cannot be seen in the Australopithecus africanus fossils from South Africa, these hominids must have been part of the Homo line not, as Johanson and White have said, a link between A. afarensis and A. robustus. A. afarensis, according to Olson, didn't exist. The presence of both Homo and robust australopithicines at Hadar is what Johanson himself originally suspected (and suggested in NATURE in 1976); and indeed. Olson notes, it was the inflated mastoid that Johanson cited as evidence of robustness. If one accepts the evolutionary scenario proposed by Johanson and White. Olson says, one must believe that Homo and A. africanus derived the gracile skull independently and that an evolutionary flip-flop occurred on the line to A. robustus, which has the same inflated mastoid.

Olson is receiving support from scientists studying other characteristics of the hominid skulls. Yves Coppens, director of the Musee de l'Homme in Paris, the mentor of Tardieu and Senut, and an original cosigner on the paper identifying A. afarensis as a species, has now reversed himself; based on the dental evidence - specifically the existence of both single-cusp and bicuspid premolars in the sample he says there must have been two species coexisting at Hadar. In addition, Dean Falk of the University of Puerto Rico and Glenn Conroy of Brown University in Providence, R.I., have been studying the venous drainage patterns seen in hominid fossils—the way the blood gets from the brain through the skull on its way back to the heart—and they say they have evidence to bolster Olson's view that the gracile australopithecines must be moved onto the Homo line.

Hominids show two distinct patterns of sinuses for blood drainage, Falk says, and the pattern seen in almost every *A. robustus* fossil and in the Hadar material (she cites the work of Kimbel and Ralph Holloway of Columbia University in New York, who have studied those skulls) cannot be found in any *A. africanus* specimens and is very rare in modern humans and apes. Falk postulates that early hominids encountered a problem with venous drainage when they became bipedal and that

different species solved the problem in two different ways; both adaptations worked perfectly well, but in terms of evolutionary scenarios, she says, the evidence indicates that the human condition must be traced back through the gracile A. africanus line to Hadar. Holloway agrees (and said so in NATURE in early June), though he gives no functional explanation for the different sinus patterns.

Another line of evidence also supports Olson's view, Falk says. She has been studying detail on the inside of hominid skulls, and has found variation in a particular sulcus, or groove, which has been taken to indicate rudimentry reorganization of the neocortex. Combined with the venous drainage evidence, the sulcus pattern divides the hominids into three groups: the robust australopithecines (and most likely some of the Hadar material) has an ape-like brain and the odd sinus; later in the gracile stralopithecines, the ape-like brain still exists but the human sinus pattern has evolved; finally the first truly human brain (based on the evolved sulcus) can be seen in combination with the human venous pattern. Holloway, however, who has had a long-running dispute with Falk about whether australopithecine brains show reorganization or not, also says that he has evidence of some neurological reorganization in the Hadar material as well.

Kimbel disputes all of the cranial evidence arguing against *A. afarensis*. Olson, he says, has zeroed in on one trait, the mastoid, while ignoring a host of cranial characteristics in the larger Hadar material "that scream primitiveness." Olson, he adds, has an insufficient appreciation for the normal range of variation in the mastoid, not only in extant African apes but also in the fossils; an enlarged mastoid has nothing to do with posture, he says, and is not a derived trait at all.

Concerning the venous drainage, Kimbel agrees with the evidence (indeed, he has found the same variability himself), but he disagrees with the way Falk and Conroy are interpreting it. Rather than co-evolving with bipedality, the two drainage patterns are "neutral adaptations" resulting from a well-known genetic phenomenon called "genetic hitchhiking," Kimbel says. Certain genes are linked physically on the chromosome, although they are unrelated in terms of function, Kimbel says, and when the genome undergoes reorganization — as when a hominid population speciates — certain traits result which have no adaptive significance. As evidence for this argument, Kimbel notes that he has studied several Homo sapiens populations, and has found that the frequency of the odd drainage pattern ranges from 6 percent to as high as 28 percent. Because the trait has no evolutionary significance, Kimbel concludes, it shouldn't be used in making taxonomic distinctions among lineages. Falk says that Kimbel is trying to explain away an embarrassing finding — one which points to a very long *Homo* lineage. Holloway says Kimbel may be right.

White and Johanson, who are the dental experts in the Cleveland-Berkeley group, also dismiss the views of Olson and Coppens. What Olson has interpreted as a sign of primitive dental morphology in one of the smaller Hadar jaws is actually the result of normal dental wear, White contends. "If you took a sample of people off the New York subway, you'd find that some wore their teeth more than others. So do you assign them to two lineages? Of course not. You've got to recognize normal variation." In another case, White says, Olson has assigned one of the largest jaws in the sample to the gracile species, simply because he failed to realize that the base of the jaw had been broken off.

White and Johanson also say that Coppens' evidence from the premolars is simply wrong. Lucy does indeed have a primitive premolar with a single cusp, they say, but the same condition can be found in very large jaws. "What we've probably got," Johanson suggests, "is a species in transition from an ancestor characterized by having single-cusp premolars to descendants — including A. africanus and Homo — that are characterized by having two-cusp lower molars. In any species in transition, some individuals will have the ancestral characteristic and others will have the derived."

More to the point, argue Johanson, White and Kimbel, the critics have failed to address the evidence they have presented for their phylogenetic tree. An entire suite of facial, dental and mandibular traits, they argue, can be seen evolving as A. afarensis developed the complex and rugged masticatory apparatus seen in A. africanus, which becomes even more rugged in A. robustus. If A. africanus is taken off the robust line, they say, it is necessary to have both the robust line and the more gracile Homo lineage deriving the identical masticatory complex. They consider that possibility highly unlikely. Furthermore, White says, if you break up the sexually dimpophic A. afarensis into two species, you're left with large-bodied, ground-dwelling hominoids with no sexual dimorphism - something that is inconsistent with everything from the earlier Miocene period and with most modern

So is it one thing or two things? In Johanson's *Lucy*, chapter 14 is titled "The Analysis Is Completed" — a title many anthropologists now see as wishful and inaccurate. The analysis continues, and most likely will for some time. Most scientists who have seen the evidence say that the Cleveland-Berkeley group has put together a powerful argument based on the cranial and dental evidence and that the burden of proof still lies with those who would unseat *A. afarensis*. Even the critics don't argue that point; but the proof, they say, is starting to mount.

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