We have still not found the missing link between us and apes

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By Colin Barras 18 May 2017

The average missing person's inquiry begins with a few vital facts. Investigators often know when and where the missing party was last seen. They might have photographs that tell them what the missing person looks like, and they usually have a name to put to that face.

Now imagine beginning a similar sort of inquiry with none of this information.

About 150 years ago, when Charles Darwin published his theory of evolution through natural selection, scientists began to accept that humans – for all our sophisticated behaviour – belong to the same family tree as all other animals.

The idea led to two inescapable conclusions. First, our species is not an only child. Somewhere out there in the natural world, there is at least one species of animal that is more closely related to humans than any other – what biologists would come to call humanity's "sister species".

Secondly, and as importantly, our species has a long-lost parent. It stands to reason that if humanity has one or more sisters, then these siblings must have shared the same parent species at some point in prehistory. Evolutionary biologists call this species the "last common ancestor" (LCA). Most people know it by a non-scientific name: the "missing link".

Scientists have been on the trail of the LCA for decades, and they still have not found it. But many are convinced that they have established enough information to make the hunt a lot easier. They think they know roughly when and where the LCA lived. They even have a reasonable idea of what it looked like and how it behaved.

Even before Darwin formalised the idea of evolution through natural selection, it was clear that humans were primates – although earlier scientists did not think this categorisation had any evolutionary implications.

> Apes in general represented evolutionary staging posts on the road to humanity

Darwin himself was initially reluctant to directly address human evolution. He barely mentioned the subject in his famous book *On the Origin of Species*.

Darwin's colleague, Thomas Henry Huxley, was perhaps the first to try to identify humanity's roots using well-reasoned evolutionary thinking. In his 1863 book *Evidence as to Man's Place in Nature*, Huxley said it was "quite certain", anatomically speaking, that humans are most similar to gorillas and chimpanzees. One of these two must be humanity's sister species, although Huxley was not sure which.

Huxley's ideas had a significant impact on 19th and early 20th Century evolutionary biologists. Many enthusiastically embraced the idea that chimps or gorillas – or even both – were our sister species. But they went further. To these biologists, it seemed that apes in general represented evolutionary staging posts on the road to humanity.

"Lesser" apes like the gibbons offered a window into the anatomy of our earliest ape ancestors. Meanwhile the "great" apes – gorillas, chimpanzees and orangutans – showed the anatomical features our ancestors possessed at the moment they split away from the other apes and began to develop a uniquely human appearance. Gorillas and chimps were not simply our sister species: they were also a lot like the LCA.

"The post-Darwinian 'paradigm' adopted living chimpanzees as stand-ins for the LCA," says Tim White, a palaeoanthropologist at the University of California, Berkeley.

This led to some very particular ideas about how the LCA looked and behaved. Primates in general (particularly monkeys) are often relatively small-bodied, and they scamper around in forest canopies by running along branches. But apes are unusual primates. Most have big bodies with extraordinarily long arms. They often get around by swinging below branches rather than running along the top of them – a form of locomotion called "brachiation".

According to many of these early researchers, the LCA was a large-bodied, long-armed, brachiating ape.

By the late 1960s, researchers were fleshing out the LCA even further. An anthropologist called Sherwood Washburn pointed out that chimpanzees, and particularly gorillas, actually spend significant amounts of time moving around on all fours on the forest floor.

> Humans just are not particularly "evolved"

Both apes use their arms in an idiosyncratic way when they walk: they flex their fingers so that their weight bears down on the knuckles. To Washburn it made sense that the LCA "knuckle-walked" too. The behaviour could even be seen as a stepping-stone on the way to walking upright on two legs, he wrote.

But it would be wrong to think that everyone was on board with these ideas of a brachiating, knuckle-walking, chimp-like LCA. In fact, almost from the moment that Huxley first put pen to paper, a minority of scientists were arguing that the earliest human ancestors – and the LCA – was decidedly not chimp-like.

For instance, just a decade after Huxley's book, biologist St George Mivart argued that humans shared many features in common with monkeys or even lemurs. Meanwhile, from 1918 onwards an anatomist called Frederic Wood Jones argued that humans had a lot more in common with tarsiers than with chimpanzees or gorillas.

Lemurs, tarsiers and monkeys are primates, but they have been evolving independently of the apes for tens of millions of years. How could anyone argue that humans are closely related to these groups? There is a simple and astonishing explanation, wrote anatomist William Straus in the 1940s. Humans just are not particularly "evolved".

It might seem absurd to argue that our highly developed brain is anything other than an example of primate evolution pushed to the extreme. But human arms, hands, legs and feet are not as highly specialised as we might assume.

"In these characters man finds his counterparts not in anthropoid apes [gorillas, chimpanzees and orangutans] but in animals that are clearly regarded… as more primitive," wrote Straus.

> The more ancient the divergence between species, the more time those species have had to accumulate their own molecular differences

What Straus and a few others were really getting at is that humans show none of the specialised features that allow other apes to swing through the trees. It made sense to at least consider the possibility that humans split apart from other primates before the apes evolved brachiation, or knuckle-walking for that matter.

Straus could not say exactly which species should be recognised as our sister. But the LCA could well have been a relatively small-bodied primate that ran along branches rather than swinging beneath them.

This disagreement continued for several more decades, says Nathan Young at the University of California in San Francisco. In fact, even into the 1980s it was not clear from anatomical features alone exactly where humans slotted into the primate evolutionary tree.

Then, just a decade later, this uncertainty vanished. By the late 1990s, almost all evolutionary biologists were willing to accept that chimpanzees, and their close relatives the bonobos, together form humanity's sister species.

To understand this turning point in the story, we have to skip back a few decades and look at what was going on in a completely different branch of science.

In 1960, Nobel-Prize-winning chemist Linus Pauling accepted an invitation to write a paper in a special scientific volume dedicated to Albert Szent-Györgyi, the discoverer of vitamin C. Working with his colleague, Emile Zuckerkandl, Pauling developed a truly revolutionary idea: the molecular clock.

> Ramapithecus was discovered in Pakistan and dated to about 14-16 million years old

"It was a revival of an idea proposed by bacteriologist George Nuttall in 1904, that if you compared blood serum you could get a sense for the evolutionary closeness of species," says Jeffrey Schwartz, a physical anthropologist at the University of Pittsburgh in Pennsylvania, US. "Their paper articulated the assumption that molecules are constantly changing, and the more ancient the divergence between species, the more time those species have had to accumulate their own molecular differences."

Pauling and Zuckerkandl used this concept – that some molecules accumulate tiny changes at a steady rate – to analyse proteins in human and gorilla blood. From the number of differences between the two sets of molecules, and an estimate of the rate that those differences accumulate, the researchers calculated that humans and gorillas had last shared a common ancestor roughly 11 million years ago.

Anthropologists were unimpressed. Only fossils could tell us when common ancestors lived, they

argued. Many reportedly described Pauling and Zuckerkandl's concept as crazy. But the molecular scientists stuck at their work and, a few decades later, they won over the sceptics – due in no small part to new fossil finds.

All manner of fossil primates, including apes, had come to light by the 1960s. One of them, an ape called *Ramapithecus* or sometimes *Sivapithecus*, had begun to look a lot like a direct human ancestor.

"*Ramapithecus* was discovered in Pakistan and dated to about 14-16 million years old," says Schwartz. "It had thick enamel, which is a feature we see in humans and their immediate ancestors." In contrast, chimps and gorillas have a thinner coating of enamel on their teeth.

> The molecular people said 'See? We were right all along!'

By 1964, palaeoanthropologists were even prepared to speculate that *Ramapithecus* walked on the ground like a human and used tools to prepare its food. And if the 14-million-year-old *Ramapithecus* really was a human ancestor, gorillas and humans cannot possibly have shared a common ancestor just 11 million years ago, as Pauling and Zuckerkandl were suggesting.

But these conclusions about *Ramapithecus* came almost exclusively from a study of the ape's teeth, which were more or less the only parts of the ancient ape that had been unearthed by the 1960s. In the early 1980s, more *Ramapithecus* fossils were unearthed, including fragments of the face. They showed that the ape looked like an orangutan, not a human.

Palaeontologists were astonished, but molecular scientists were not. By now they had established that humans, chimps and gorillas were all closely related and shared a common ancestor within the last 11 million years or so, and that orangutans were slightly more distant relatives with a deeper prehistory. According to their thinking, a 14-million-year-old ape would be unlikely to look distinctly human, because it predated the appearance of the human lineage. But it might well look orangutan-like.

"The molecular people said 'See? We were right all along!'," says Schwartz.

In the 1980s and 90s, the molecular community built on such successes.

More sophisticated molecular techniques became available, allowing the scientists to compare apes in minute detail at the genetic level and work out which were most closely related to humans.

"The gorilla held out as a pretty good candidate," says Owen Lovejoy, an anthropologist at Kent State University in Ohio. "But eventually the chimpanzee won out."

> By seven million years ago the European and Asian apes had vanished

Final confirmation that chimpanzees (and the closely related bonobos) are humanity's sister came in 1997, and it seemed to some that the LCA debate was drawing to a close. Huxley's work in the 1860s had encouraged many scientists to see the LCA as chimp-like, and the molecular work of the 1980s and 90s seemed to vindicate the idea.

"There began to be a more general acceptance of the implications that the LCA was likely to be more chimp-like," says Young.

This was not the only conclusion from the molecular work. The DNA studies also put an approximate date on the human-chimpanzee split: six or seven million years ago. It was a figure that considerably narrowed down the search for the LCA.

The fossil record shows that apes were widespread across Africa, Europe and Asia about 20 million years ago – at this time the world really was the Planet of the Apes. But by seven million years ago the European and Asian apes had vanished. If chimpanzees and humans split at this time, the LCA must have lived in Africa – in the same sort of environments occupied by modern chimps.

By the early 2000s, some physical anthropologists were even describing African apes like the chimpanzee as time machines into the earliest stages of human evolution.

The story should end there, but it does not. Surprisingly, the last 15 years has actually seen popular opinion begin to swing away from the idea of a chimp-like LCA, and towards a model closer to that argued by people like Straus in the 1940s.

There are several factors that explain the recent rethink. A more thorough understanding of chimp and gorilla anatomy helped.

There had been murmurings for some time that gorillas and chimpanzees (and bonobos) might not knuckle-walk in quite the same way. In 1999, Mike Dainton and Gabriele Macho at the University of Liverpool, UK, looked at the idea more formally. From subtle differences in the way gorilla and chimpanzee wrist bones change as the apes grow from juveniles to adults, Dainton and Macho concluded that the two may have evolved knuckle-walking independently.

Over the following decade, other researchers reported similar findings. By 2009, Tracy Kivell – now at the University of Kent, UK – and Daniel Schmitt at Duke University in Durham, North Carolina, were arguing that humans did not evolve from a knuckle-walking LCA.

Kivell says the 2009 paper received quite a lot of attention. She thinks this might be because it was published just a few months before one of the most complete and potentially important fossils for understanding human evolution was officially unveiled – one that some people think blows a huge hole in the idea that the LCA was chimp-like.

Late in 2009, a research team including Tim White and Owen Lovejoy published a collection of research papers describing the remarkably well-preserved skeleton of "Ardi" – a 4.4-million-year-old fossil of the species *Ardipithecus ramidus*, which White and his colleagues had discovered in Ethiopia.

> Put simply, Ardi looked "primitive"

White and Lovejoy's careful analysis strongly suggested that Ardi habitually walked on two legs when she was on the ground. It was one of many features that suggested to them that Ardi

should be considered an early human, or hominin – one that lived just a few million years after the LCA, and so provides us with our best idea yet of exactly how it looked.

This conclusion was significant, because in many respects Ardi's anatomy is not at all chimp-like. It is very unlikely she was either a knuckle-walker or a brachiating ape.

Ardi lived in a forest setting and must have spent time in trees as well as on the ground. But her anatomy suggests she was adapted to move around in those trees almost like a large monkey might, moving cautiously on feet that – unlike gorilla and chimp feet – seem to have been unsuitable for wrapping around branches for grip.

Put simply, Ardi looked "primitive" – and that suggested that the LCA looked primitive too.

Of course, the Ardi analysis was not uncontroversial. One of the implications of their interpretations was that all sorts of anatomical features shared by gibbons, orangutans, chimps and gorillas must have evolved independently in each of these apes.

> People have begun to question what was an emerging consensus

"I think they took it a little too far," says Kivell. "Their model means that there is a lot of parallel evolution across all apes. I still think comparative studies with chimps and other African apes can provide a lot of insight into our own evolution."

Sergio Almécija at the George Washington University in Washington DC agrees. "I do believe that chimps could represent good models for the LCA for certain aspects – for instance body size, perhaps cognition," he says. But his own research has also helped to emphasise that chimps might not simply be living time machines from the time that the LCA was alive.

In 2015, for instance, Almécija and his colleagues published an analysis of ape hands that emphasised just how much the length of digits has evolved in chimpanzees since they split from the LCA. Judging by fossil evidence from earlier apes, human hands are surprisingly primitive in appearance – notwithstanding the fact that we evolved an opposable thumb after the split from the LCA.

Even the biologists studying modern primates are finding evidence that the LCA may not have been chimp-like.

In one 2013 study, Pavel Duda and Jan Zrzavý at the University of South Bohemia in the Czech Republic used what is known about living ape behaviour – and about the shape of the ape evolutionary tree – to try to estimate when certain traits first evolved. They suggested that sexual intercourse lasted longer in the LCA than in chimpanzees, and that the LCA males devoted more time to looking after offspring than chimp males do.

> Apes were still flourishing in Europe as well as Africa 13 million years ago

Decades after Straus and a few other anatomists had argued that the chimpanzee was a poor model for the LCA, mainstream opinion has moved their way. "There has been a community shift, where people have begun to question what was an emerging consensus for a chimp-like LCA,"

says Young.

But even that is not the end of the story. There are still "chimp-like LCA" advocates out there, and they are fighting back.

For instance, in 2015 Young and his colleagues argued from the study of ape shoulder blades that the LCA might have had some features in common with chimps and gorillas after all, hinting that it might actually have been a brachiating ape. Such a conclusion would not have been controversial if it had been published a decade or so ago, Young says – but mainstream thought has shifted so far from the chimp-like LCA concept that the paper did, in fact, face some criticism.

Of course, only if and when fossils of the LCA itself come to light will the debate finally draw to a close. But the search for those crucial fossils is no longer quite as straightforward as it once seemed. In the last five years, some geneticists have begun to question whether the molecular clocks they use to estimate when the LCA lived are being read correctly. It is possible, they say, that the LCA might actually have lived 13 – not seven – million years ago.

Apes were still flourishing in Europe as well as Africa 13 million years ago, which means that in principle the LCA might have lived there.

Possible support for that idea comes from a 2015 analysis of an ape called *Dryopithecus* that lived in both Africa and Europe about 12.5 million years ago. David Begun, an anthropologist at the University of Toronto in Canada, concluded that *Dryopithecus* might be an early relative of the gorilla, and suggested that the LCA of humans and chimps might consequently have lived about 10 million years ago.

"It is not impossible that the LCA was European," says Begun – although there is no direct evidence for that yet, and he still favours the idea it was African.

There are also a few researchers who take a completely different view.

> There is not yet universal agreement

For instance, Schwartz is adamant that it is orangutans, not chimpanzees, that are our sister species. It is an idea he first developed in the 1980s – before, he says, anthropologists "caved in" and conceded that molecules and not anatomy were the ultimate arbiters of the shape of the ape family tree.

Schwartz thinks DNA is not the infallible witness on evolution many assume it to be, and that there are many anatomical and behavioural similarities between humans and orangutans that should not simply be ignored. For instance, both have thick layers of enamel on their teeth, and female orangutans (like women) do not "advertise" to males when they are most fertile – something biologists call oestrus. "Orangs are the only other mammal I know of that don't have oestrus," says Schwartz.

To be clear, few researchers agree with Schwartz. But even putting his ideas to one side, it is clear that there is not yet universal agreement on the LCA.

It is true that, today, some researchers have a well-thought-through idea of what the LCA looked like and how it behaved. The trouble is that other researchers have equally well-reasoned models that suggest an LCA that looked and behaved in a completely different way. And that puts the research community in a bit of a quandary.

In principle, fossilised remains of the LCA might come to light any time. They might even be discovered this very year. But because there is so little agreement on what the LCA should look like, researchers will interpret the fossils differently.

"It's a problem that we might encounter," says Almécija. "Are we going to be able to recognise the LCA when we find it?"