

The conventional portrait of human evolution—and, indeed, of the history of life—tends to be one of lines of ancestors and descendants. We concentrate on the events leading to modern humanity, ignoring or playing down the evolution of other animals: we prune away all branches in the tree of life except the one leading to ourselves. The result, inevitably, is a tale of progressive improvement, culminating in modern humanity. From our privileged vantage point in the present day, we look back at human ancestry and pick out the features in fossil hominids that we see in ourselves—a bigger brain, an upright stance, the use of tools, and so on. Naturally, we arrange fossil hominids in a series according to their resemblance to the human state. *Homo erectus*, with its humanlike, upright stance and big brain, will be closer to us than *Ardipithecus ramidus* or *Australopithecus afarensis*, which had smaller brains and more apelike features.

Because we see evolution in terms of a linear chain of ancestry and descent, we tend to ignore the possibility that some of these ancestors might have been side branches instead—collateral cousins, rather than direct ancestors. The conventional, linear view easily becomes a story in which the features of humanity are acquired in a sequence that can be discerned retrospectively—first an upright stance, then a bigger brain, then the invention of toolmaking, and so on, with ourselves as the inevitable consequence.

New fossil discoveries are fitted into this preexisting story. We call these new discoveries 'missing links', as if the chain of ancestry and descent were a real object for our contemplation, and not what it really is: a completely human invention created after the fact, shaped to accord with human prejudices. In reality, the physical record of human evolution is more modest. Each fossil represents an isolated point, with no knowable connection to any other given fossil, and all float around in an overwhelming sea of gaps.

When Darwin was thinking about mechanisms for evolutionary change, one of his problems was the lack of sufficiently long intervals of time for his schemes to work. He saw evolution as generally slow and gradual yet the scholarship of his time viewed Earth as no older than the few thousand years allowed in the Bible. The realization, by

Victorian geologists such as Darwin's geological mentor, Charles Lyell, that Earth was inconceivably, if not immeasurably old, gave Darwin's idea of natural selection time enough to change one species into another, all the way from the primordial slime to the flora and fauna we see around us today.

In *The Origin of Species*, Darwin put the case for natural selection—his mechanism of evolution—by analogy. Given a group of creatures varied in shape, behaviour, and other attributes, natural selection picks those variations most suited to the prevailing environmental conditions, in the same way that pigeon fanciers select the animals with features closest to the desired traits and use these animals as breeding stock. Give a pigeon fancier a well-stocked pigeon loft and enough time, and he could produce pigeons as varied as pouters, tumblers, and fantails. By analogy, give nature a palette of protoplasm on the early Earth and the full span of geological time, and she could produce pigeons, pigeon fanciers, and everything else.

The analogy between rearing pigeons and natural selection is, however, incomplete. Pigeons bred to be tumblers, pouters, and fantails are still pigeons. At no point does the breeder produce a breed of pigeon that is so extreme that one can no longer consider it a pigeon. In Darwin's analogy drawn from fancier's records, endless varieties can be produced but in no case are new species formed. Artificial selection takes place against the continuity of ordinary, everyday time. Natural selection as devised by Darwin—this force that changes one species into another—does not happen within this timescale.

If this assertion seems rather sweeping, take a look at your own ancestry. Look again at those old family photographs: do any of your ancestors look any more apelike than you? No, they do not. But just suppose they did: would you expect any apelike traits to be more marked the further you look back in time? Of course not. If, like me, you are unable to trace your ancestry back more than three or four generations and therefore test these wild and distasteful notions, you might seek solace in more illustrious pedigrees. Queen Elizabeth II, for example, can trace her ancestry back more than a millennium, past the Norman Conquest, back to the Anglo-Saxon chieftains of Wessex. Yet there

is no evidence that Alfred the Great was any less human or more ape-like than the present sovereign. So where does this evolution happen?

Let us look at the problem another way. My cat, Fred, is a fine specimen of an oriental lilac Siamese. As a product of artificial selection by cat fanciers, he has the pedigree to prove it. His ancestry can be traced to his great-great-great-grandparents, all thirty-two of them, and those are only the ones with names that can be written comfortably on the breeder's certificate. Some of these ancestral cats were show champions, officially the finest examples of their breed. No doubt, then, that Fred's ancestors are cats—and cats, by definition, with certificates and rosettes to prove it. Fred's pedigree, like mine, while perhaps showing signs of artificial selection, shows no sign of evolution either. Why?

In ordinary, everyday time, the generations of Fred and me run on the separate, parallel tracks, respectively, of feline and human generations, neither converging nor diverging. But in Deep Time, species are malleable, and the parallel lines converge. But how can this be, if my ancestors were all human, and Fred's were all cats?

In ordinary time, organisms such as people, pigeons, and cats breed true to their kind. Deep Time, in contrast, is time enough for species themselves to transmute. Deep Time is the key to the origin of species, because intervals of time of geological extent were required for Darwin's mechanism—natural selection—to do its work and change one species into another. Evolution is a consequence of Deep Time.

Although Fred and I are different in many ways, we have much in common, signs of a shared evolutionary heritage. At some unspecified location in Deep Time, there was a creature, our latest common ancestor, from which the lineages leading to Fred and me diverged, each going on its own separate course.

The problem is that Fred and I cannot place our common ancestor in time and space unless we are able to discover our complete pedigrees all the way back to that point of ancestral convergence. To do this, as we know, is impossible, given that the fossil record is so discontinuous. All we know is that she existed—sometime, we know not when; somewhere, we know not where. It is conceivable that we could dig up the fossil remains of our latest common ancestor. But even if we

did, we could never know that we had done so. But we can still get some idea of what our latest common ancestor was like, even without fossil evidence.

The evidence of evolution is everywhere around us, in the signs that diverse organisms share a common morphological heritage. That Fred and I have a common ancestry is not in dispute, not because of fossils, but because of features we share thanks to our common evolutionary birthright.

For all our superficial differences, Fred and I are very similar underneath. We both have backbones made of stacks of vertebrae, and skulls enclosing our brains and protecting our paired eyes and ears. We share these features thanks to a common ancestry going back more than 500 million years, to when the first vertebrates—backboned animals—appeared in the sea. The earliest fossils of vertebrates are just scaly flakes and fragments. Even so, we know just by looking at Fred and me, and knowing that all vertebrates have a backbone, a skull, and paired sense organs, that our common ancestor must have had these features, too.

Yet Fred and I share features indicating a more exclusive common ancestry than that indicated by the shared possession of the characteristics of vertebrates. We both have tooth-bearing jaws, and two pairs of fleshy limbs. The shared heritage of limbs in this pattern marks Fred and me as not only vertebrates but 'tetrapods'. All tetrapods are vertebrates, but not vice versa: we have two pairs of limbs in addition to the backbone, skull, and sense organs, making us members of a more exclusive group. The latest common ancestor of Fred and me must have had these shared features, acquired along evolution's journey.

But Fred and I share yet further characteristics, indicating a still more exclusive common ancestry. Not only do we have a backbone, a skull, paired sense organs, four limbs, and so on; we also (thanks to our shared heritage) benefitted, as embryos, from the protection of membranes, which protected us from drying out, kept us fed with yolk, and looked after our bodily wastes. One of these membranes is called the 'amnion'. As a result, Fred and I are both 'amniotes'.

Our common heritage is more exclusive still: we both have hair and

a highly regulated metabolism that keeps a constant body temperature. We also share a lot of little details about our anatomies, such as the precise way that our jaws hinge onto our skulls. We also, when we were very young, suckled milk from our mothers from organs provided for the purpose; our mothers had previously nurtured us in wombs, rather than laying eggs (which some amniotes, such as reptiles and birds, generally do). By virtue of all these shared features, both Fred and I are mammals.

Our latest common ancestor must, therefore, have been a mammal, too. Long ago, in some long-lost crevice, a mammal had a litter of progeny, which went their separate ways to seek their fortunes. One founded a lineage whose end result is me. Another multiplied to produce the dynasty of which Fred is the latest scion.

When did our most recent common ancestor live? Where? What was she like? We cannot reliably know the answers to the first two questions, but we can get some idea of the third, simply by comparing the features that Fred and I share. She was a warm-blooded furry animal that bore live young and suckled them.

We cannot paint a more complete portrait. Although our common ancestor had four legs and a tail, we cannot know how long her tail was, or the colour of her fur. Although we know that she had paired eyes and ears, we don't know whether those eyes were blue, green, brown, or pink, or if her ears were rounded or pointed. Although she had teeth, we do not know if they were like Fred's feline fangs, my own more modest molars, or like something else instead, of a shape that no longer exists in any living animal. Perhaps our common ancestor was a ratlike creature. Or perhaps not. We will never know, because in the intervals of Deep Time since those long-lost litter mates left the nest, evolution gave each lineage its own distinct inventory of features, the history of which explains why Fred is a cat and I am a human. This can all be summarized as a simple diagram (see figure 2).

This is not a genealogy. It is not an explicit family tree. All it does is summarize the tale about the acquisition of features, showing that Fred and I represent two separate lineages that diverged beyond a 'node'. There is an important distinction to be made between this dia-

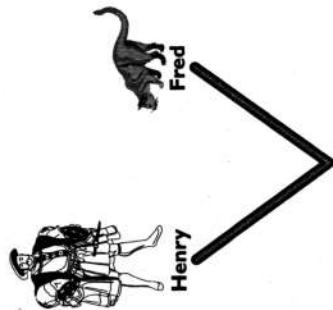


Figure 2. How the ancestries of Fred and myself are linked, through Deep Time, with our common ancestor at the 'node'. (Diagram by Majo Xeridat)

gram and an explicit genealogy. In a genealogy, the node would represent a real individual.

In this diagram, the real individuals—the ones we can know about—appear at the tips. The node represents an ideal state: not the common ancestor by name, but the inventory of shared features, acquired in evolution, which we would expect it to have, given what we know about Fred and me.

That Fred and I really did have a common ancestor is not in doubt, but we cannot hope to find her as a fossil; or, rather, if we were to find her, we could never know for certain that we had done so. This principle is reflected in the diagram, in the form of the node linking my ancestry with Fred's. The node reflects a notional embodiment of the inventory of features shared by Fred and me; and that is all. It says nothing about when our latest common ancestor actually lived, or where.

Neither can the diagram tell us about any features that made that common ancestor distinctive in her own right. For all we know, our shared common ancestor had features peculiar to herself, none of which are present in either Fred or me, and which are lost forever. All the node does is mark a way point in Deep Time, the point when the heritage shared by Fred and me gave way to separate and divergent histories. Importantly, it doesn't matter whether the lines linking me, Fred, and the node are short or long, or of different lengths or thick-

nesses. It doesn't matter whether the angle joining them is obtuse or acute. All that matters is the way they are joined—the topology.

Having established all that, the diagram in figure 2 doesn't do anything besides express a truism that Fred and I have a common ancestor, and that we are cousins in some unknown degree. If life had a single origin, then every organism that ever existed, alive or dead, is a relative of every other organism, alive or dead. Even if we can never know that Yorick, the fossil I hold in my hand, is my direct ancestor, we can be sure that he is my cousin, yours, or Fred's. You can, with equal facility and justification, find any two creatures, living or extinct, and draw a diagram as in figure 2 to express their shared common ancestry. In which case, a diagram expressing the common ancestry of any two living creatures is always true.

There is, however, a more constructive way to explore the relationship that I have with my cat Fred. Rather than state that any two organisms are cousins to an unknown degree, we can try to estimate this degree, at least in relative terms. To do that, we need to introduce some perspective in the form of another participant.

My other cat, Marmite, unlike Fred, has the breeding and manners of an alley cat. Her pedigree is even less well established than mine, let alone Fred's. Even so, Marmite and Fred have a lot in common. Like Fred, she has pointed ears, whiskers, and retractile claws and likes to chase mice and tease the dog next door. I can claim none of these attributes.

However, all three of us like to eat fish and go to sleep in the afternoons when we have the chance. Fundamentally, we are all vertebrates, tetrapods, amniotes, and mammals. But because Marmite and Fred have more in common with each other than either does with me, we can reasonably infer that Marmite shares a common ancestry with Fred from which I am excluded; as cousins, she and Fred are closer to each other than either is to me. To put it another way, the latest common ancestor of Fred and Marmite lived later than the latest common ancestor of all three of us, although we cannot know how much later. Figure 3 expresses our mutual relationships.

The diagram in figure 3 says more than the truism expressed in fig-

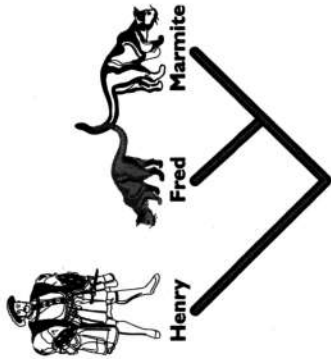


Figure 3. A diagram showing the inferred relationships between me and my cats, Fred and Marmite. (Diagram by Majo Xeridat)

ure 2. This is because it makes a particular statement about the order in which organisms are related, over and above the fact that they all share some degree of common heritage. In a topological sense, the diagram in figure 2 must always be true, because there is only one way to draw it. In contrast, there is more than one way of arranging three (or more) participants in a diagram like this, so the statement about relationships in figure 3 can be tested against possible alternatives.

This notion of testability is crucially important, because it elevates the diagram from an assertion to the status of a scientific hypothesis. A diagram of this sort is called a 'cladogram', from a Greek word meaning a branch. The business of drawing up and testing various alternative cladograms is called 'cladistics'.

In cladistics, presumptions about particular courses of ancestry and descent are abandoned as unprovable or unknowable. Yet cladistics does more than state that we are all cousins. It is a formal way of investigating the order in which organisms are cousins, by examining the possible alternatives. Cladograms are statements of collateral relationship of greater or lesser extent. Given that, they sidestep the question of whether Yorick is my ancestor, or if any fossil is the ancestor of any other, because the answer to these questions can never be known. In other words, cladistics acknowledges the discontinuities of Deep Time and, by acknowledging them, transcends them.

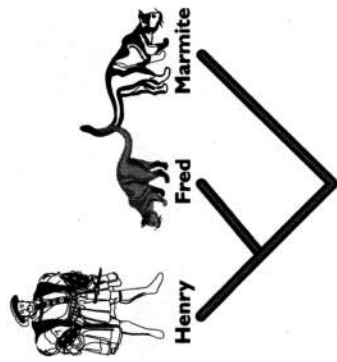


Figure 4. An alternative relationship between me, Fred, and Marmite.
(Diagram by MaJo Xeridat)

Figure 4 illustrates one of the alternatives to figure 3—an alternative cladogram—for the relationship between me, Fred, and Marmite. In this cladogram, I share a common ancestry with Fred that excludes Marmite.

If it's possible to arrange three participants in more than one way, how can one know which one reflects the actual course of evolution—what really happened? The cladogram in figure 3 seems so natural, so plausible, that it must be right. But must it? The fact that three participants can be arranged in a different way from that intuitively expected suggests that it is at least possible to conceive of different evolutionary courses. To dismiss this and assert that the cladogram in figure 3 must be right simply because it accords with native common sense, is not a scientific approach, because it allows only what we humans imagine is possible and denies us the opportunity of exploring all the alternatives and examining which one best fits the evidence at hand.

How, then, is it possible to evaluate the likelihood of different alternatives? Formally, it is not, because we cannot discover the particularities of ancestry and descent that join us together. In practice, however, we can adopt a principle that has stood science well for centuries. That is the Principle of Parsimony, or Occam's Razor: when two hypotheses present themselves, it is prudent to choose, as a working hypothesis, the one that requires the fewest assumptions to justify itself. It is important

to realise that the principle of parsimony does not select the 'right' answer—that is unknowable—but only the best one to be getting on with first. Because we cannot hope to retrieve the continuous skein of ancestry and descent that links us all, this is the best we can hope to achieve.

This is not only true in evolutionary biology, but in all science. All hypotheses are provisional and are likely to be overturned when new evidence allows a closer approximation to the truth. If this were not true, science would stop.

How can my cats and I resolve the pattern of our heritage? Looking at the cladogram in figure 3 and applying the principle of parsimony, we can explain this pattern by proposing that all those feline features that define Fred and Marmite's ancestry, to the exclusion of my own, appeared just once—somewhere between the node bracketing the two cats and the node that defines all three of us.

The situation in the cladogram in figure 4 is more complicated. If Fred and I share a common ancestry that excludes Marmite, then the catlike features that Marmite and Fred so evidently share could have evolved twice, independently, in the separate lineages leading respectively to Marmite and to Fred.

Because the cladogram in figure 3 implies that catlike features evolved only once, and the one in figure 4 implies that they might have evolved twice, parsimony favours the first. As a working hypothesis, it is simpler to imagine that all the features so characteristic of cats—the pointed ears, the whiskers, the retractile claws, the constant demands to be let into the garden (and readmitted thirty seconds later), and so on—evolved just once, rather than twice, independently. It is entirely possible that these features really *did* evolve independently, on more than one occasion—nobody says that evolution is parsimonious—but for the sake of simplicity, we choose the most parsimonious alternative for the time being, until some other evidence turns up to favour a different view.

The problem is actually more complicated, because the cladogram in figure 4 has a second interpretation. That is, the common ancestor of me, Fred, and Marmite was catlike, and these features have been lost—just once—in the lineage leading to me. This second interpretation is

just as parsimonious as the cladogram in figure 3, except that features are lost, rather than acquired. How can we decide between the two?

Sometimes it is not possible to decide between two equally parsimonious cladograms. In this case, we can break the deadlock by introducing a further element of perspective, by testing the two alternatives against a fourth participant, which, based on independent evidence, we have good reason to suspect stands outside the three of us. In cladistics, this kind of arbitrator is called an *outgroup*, and the process of arbitration, *outgroup comparison*.

I elect to use, as an outgroup, one of the pigeons that Marmite often chases out of her London garden. This is not an arbitrary choice. Like me, Marmite, and Fred, the pigeon is a vertebrate, a tetrapod, and an amniote. However, unlike people or cats, the pigeon lacks mammalian features such as hair, mammary glands and the habit of suckling infants. From this, we can assume that the latest common ancestor of the pigeon and the rest of us did not have mammalian features. Although the pigeon is a cousin to Marmite, Fred, and me, we have good reason to think that it stands at a remote remove.

Figure 5 shows the cladograms in figure 3 (on the left) and figure 4 (on the right) with the pigeon added as an outgroup. The cladogram on the left requires the evolution of catlike features only once, as it did in figure 3, in the branch leading exclusively to Marmite and Fred. However, the cladogram on the right requires *either* that these catlike features evolved in the common ancestry of me, Marmite, and Fred, but were subsequently lost in my own ancestry, *or* that they were acquired independently in the separate lineages leading to Marmite and Fred. Either there is a gain of catlike features and a subsequent loss of all these features, making two events—a gain and a loss—or catlike features were gained twice, independently, again making two events. Because they each contain two events, both interpretations of the cladogram on the right are less parsimonious than the one offered in the cladogram on the left, which requires just one event. Once again, the cladogram in figure 3 comes out as the best provisional hypothesis. As far as we can tell on the evidence we have, Fred and Marmite share a common ancestry that excludes me.

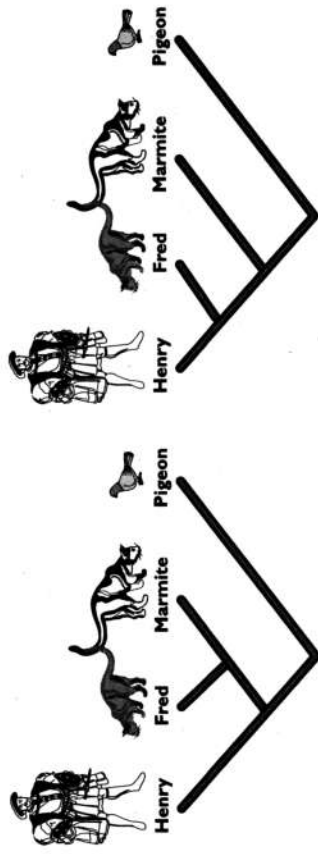


Figure 5. Adding the perspective of an outgroup (a pigeon, in this case) allows the resolution of two equally parsimonious cladograms. (Diagram by Majo Xeridat)

I am now going to do something rather mischievous, something that only cladistics allows. In figure 6 I add a fossil to the panoply of living, breathing entities in the cladogram I drew up in figure 3.

This cladogram is just like the one in figure 3 inasmuch as it concerns me and my cats. It is different in that it adds Yorick, the imaginary hominid fossil, and places it next to me. The implication is that Yorick and I share a common ancestor quite different from the latest common ancestor of Marmite and Fred. The common ancestor of Yorick and me would have had features that one does not see in cats, such as the peculiarities of hominid dentition. Even though Yorick is now less an individual than a chipped tooth, we know enough to see

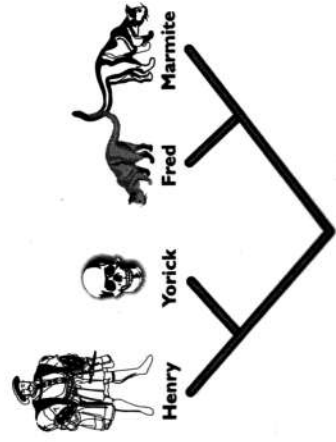


Figure 6. A cladogram with a fossil in it. (Diagram by Majo Xeridat)

that the tooth is more like my molars than Marmite's or Fred's fangs. Something about this cladogram is astonishing. It is simply that three living individuals—me, Marmite, and Fred—are found in the cladogram, on the same plane, on the same footing as a fossil, Yorick, which is not only dead, but has been so for more than 3 million years. This cladogram transcends time.

In a conventional genealogy, relationship is plotted from side to side, across the page, whereas time is drawn from the top of the page to the bottom. Conventional genealogies, then, are like the embossed rolls in a player piano: the notes are arranged in time according to the specific places where they appear on the roll as it unwinds. This cladogram seems to ignore time entirely: all it does is plot degrees of evolutionary relationship.

But it is more subtle than that. My cladogram ignores only ordinary time, the kind of time that unrolls in lengths of days or years, or a few generations, the time whose span encompasses the ancestries of Fred the cat or Queen Elizabeth II. Evolutionary change is not a feature of this kind of time, in which we descend, human to human, cat to cat, along our distinct parallel tracks.

On the other hand, the cladogram is a suitable expression of evolutionary change, independent of the particulars of ancestry and descent. It is therefore a simple expression of evolutionary relationships. As such, the cladogram asks no questions of Deep Time that it cannot answer.

Yorick, and the half-tooth he left us, were products of imagination. Yet the fragment of jaw that Robert found beneath a thorn tree was real enough, as was the sheared molar that Gabriel unhesitatingly drew from the sieve before me. These are real fossils that were once part of real individuals who existed in time and space. We are entitled to say that the fossils discovered at LO5 were our cousins to some degree—yours, mine, Gabriel's, Robert's, Nzube's, Meave's—but not to assert without question that they were, or might have been, our direct ancestors.

No matter how fragmentary or antique, the bones and teeth that Meave Leakey's team continues to unearth belonged to real individu-

als who walked the Earth as surely as Fred, Marmite, and I do today. If we cannot imagine ourselves as missing links, we are not entitled to demand this of the fossils we find. They were neither missing links nor transitional forms: they existed in their own right, not as staging posts in a preordained story between the apes and the angels.