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VIEWS FROM UNDERSTANDING EVOLUTION

Darwin's "Extreme" Imperfection?

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Darwin used the words "extreme imperfection" to refer not to any personal character flaw but to the gappy nature of the fossil record (Darwin 1859). The vast majority of organisms that have lived on Earth never fossilized. Jellyfish and worms? Too squishy to fossilize very often. Butterflies? Too delicate, for the most part. Anything that lived on mountain slopes or in fast-moving rivers? Unlikely to be covered by sediment and preserved. Darwin saw such haphazard preservation as a serious problem for the theory of evolution. After all, he was proposing that different modern species share common ancestors—that organisms as different as lobsters and butterflies have the same great-great-great-great…great-grandparent species. Direct fossil evidence of all the intermediate forms connecting an ancestor to its modern descendents would have provided undeniable evidence in favor of his theory. In Darwin's view, however, the fossil record provided no such support. Much of *On the Origin of Species* is taken up with marshalling other forms of evidence to support his ideas about common ancestry and natural selection.

In an article included in this issue (*Charles Darwin and Human Evolution*), Ian Tattersall (2009) proposes that Darwin's disparaging view of the fossil record, along with other factors, might help explain why Darwin did not write more about human evolution. Tattersall notes that some fossils shedding light on human evolution *had* been discovered at the time of Darwin's writing but that the area was tainted by fraud and controversy. Darwin may have viewed our own fossil history as just another gap in the fossil record—one which might never be filled by hard evidence. Though he clearly accepted the idea that humans evolved from ape ancestors, Darwin may have curtailed his discussion of this transition partly because of the evidence he wanted, but did not have: fossils of so-called missing links. Here, we will dig into the concept of a missing link to see whether this is the problem for evolutionary theory that Darwin imagined and to find out what we have learned about this sort of evidence since Darwin published his ideas in 1859.

Are "Missing" Links Really Missing?

When we describe something as *missing*, it usually implies that the item is supposed to be present, but for unknown reasons, no longer is. A missing person, for example, is someone who has mysteriously disappeared. But you would not describe that person as missing if you knew that he was away visiting his aunt in another city. In this way, the term *missing link* is a bit of a misnomer. Fossilization is a chancy process. Most organisms that have lived on Earth are not preserved as fossils (e.g., Fig. 1). They may be eaten or rot away after death. Furthermore, very few organisms wind up in situations in which fossilization is possible, with body parts that are easily preserved as fossils. Thus, biologists *expect* that most intervening steps of an evolutionary transition (e.g., from ancestral arthropod to modern butterfly) will not be recorded as fossils. Because we know *why*

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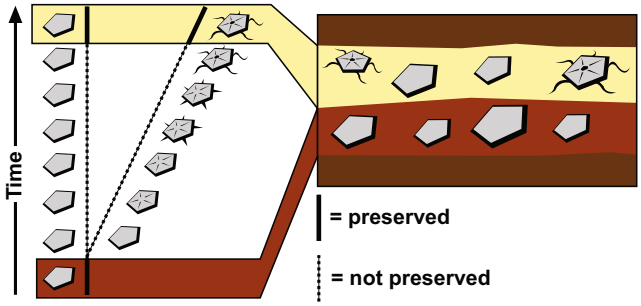

Fig. 1 Even when evolutionary change occurs slowly and steadily, many steps in the transition may not be preserved in the fossil record. Illustration adapted with permission from the Understanding Evolution website

so-called missing links do not always put in an appearance in the fossil record and because we *expect* this to be the case, missing links are not technically missing at all. Tattersall points out that Darwin was well aware of this perspective. In *On the Origin of Species*, Darwin devoted a chapter to the nature of the geological record, explaining why key transitional fossils might not be found and why we might not know about many of the links that *are* preserved.

Darwin (1859) described the lack of missing links in the fossil record as "the gravest objection which can be urged against my theory." If this was the most serious objection raised against Darwin's ideas at the time, the counterarguments must have been weak. After all, everything we know about geological processes and biology indicates that we should not expect the fossil record to provide a complete catalog of the history of life on Earth. The fact that the fossil record is, indeed, incomplete is entirely consistent with evolutionary theory. Sure, more transitional fossils would shed additional light on the evolutionary history of many lineages, but a lack of transitional fossils in no way implies that those lineages did not evolve. As we will see, the fossil record may even be more complete than Darwin imagined.

Missing Links vs. Transitional Features

Paleontologists interested in major transitions in the history of life generally prefer the term *transitional feature* to *missing link* for several reasons. First, as described above, missing links are not really missing. Second, different features of a modern organism may have evolved at different times in that lineage's history. The tetrapod transition from water to land, for instance, involved the evolution of many features—adaptations for moving, sensing, breathing, and bearing young in this new, dry environment. However, these changes did not all occur at once. For example, evidence suggests that the earliest tetrapods evolved four limbs long before they evolved an ear with an eardrum adapted for sensing vibrations through the air (Clack 2002). This means that the fossil organisms that represent the transition from fin to leg may not be the same organisms that most clarify the evolution of modern tetrapod ears. Hence, in many cases, it is more accurate to focus attention on a specific transitional feature than on an organism as a whole.

Finally, the term *missing link* implies that the fossil under consideration represents a direct ancestor of the modern organism of interest—a link in the genealogical chain between ancestor and descendent. However, the fossils that paleontologists study to understand evolutionary transitions most often represent close relatives of those ancestors, not the ancestors themselves. That is because finding those direct ancestors in the fossil record is extremely unlikely, given the vagaries of fossilization and the ubiquity of extinction. More than 99% of the species that have ever lived on Earth have gone extinct. Hence, most of the fossils we discover represent lineages that were cut short. Nevertheless, these ancient relatives are extremely valuable to science since they often display the same transitional features that the direct ancestors must have had. They illustrate the steps taken by evolution between ancestor and descendent and can help us understand the order in which new traits evolved and how they functioned as they did so. Figure 2 illustrates the difference between direct ancestry (a) and the more typical relationship fossils with transitional features have to their modern counterparts (b).

The recent discovery of *Tiktaalik* (Daeschler et al 2006), a 375 million-year-old fossil, represents one of these cases—though it was frequently portrayed in the media as a "missing link." *Tiktaalik* is technically a fish. It had scales, gills, and fins with delicate ray bones, like most fish. And like fish, it lacked an eardrum for sensing air vibrations. However, *Tiktaalik* also had characteristics that we associate with land-dwelling vertebrates: sturdy

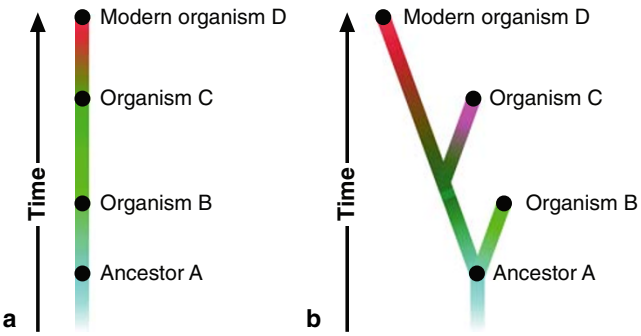

Fig. 2 Phylogenies illustrating the difference between **a** direct ancestry and **b** the more typical relationship fossils with transitional features have to modern organisms

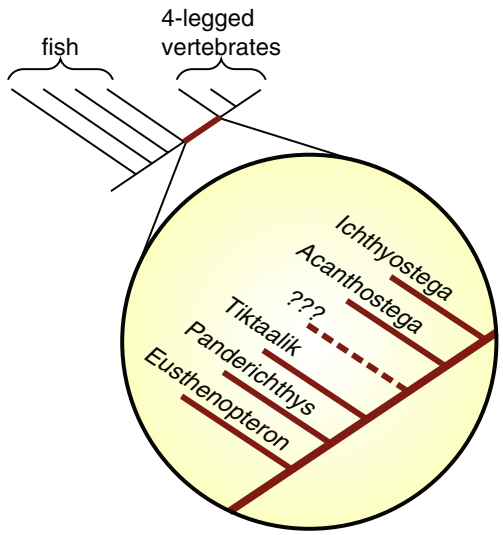

Fig. 3 Many fossil organisms exhibiting transitional features help illuminate the origin of land-living vertebrates. As suggested by the dashed line, some have yet to be discovered. However, these organisms are not the direct ancestors of modern tetrapods. Illustration adapted with permission from the Understanding Evolution website

wrist bones, thick ribs, flattened head, a neck, and shoulders. *Tiktaalik* probably lived in shallow water, propping itself on the bottom and snapping at prey. The adaptations it had for this way of life wound up providing the stepping stones for vertebrates to climb onto dry land. In fact, scientists have discovered a series of organisms with transitional features (e.g., *Eusthenopteron* and *Acanthostega*) that tie fish to four-legged vertebrates. None of these organisms were the direct ancestors of modern tetrapods (see Fig. 3)—but they were closely related to those ancestors and provide vital information about the characteristics those ancestors had.

Although fossils exhibiting transitional features do not generally represent the direct ancestors of modern organisms, there are, of course, exceptions. In fact, some paleoanthropologists argue that many of the fossils we have discovered from our own genus, *Homo*, represent our direct ancestors. This issue was recently highlighted by the discovery of two fossils: a 1.44 million-year-old jawbone, hypothesized to have belonged to *Homo habilis*, a big-brained toolmaker, and a 1.55 million-year-old skullcap attributed to *Homo erectus*, which may be one of our own direct ancestors (Spoor et al 2007). Scientists are considering at least two hypotheses regarding the relationship between these species (Gibbons 2007): *H. habilis* may have given rise to *H. erectus*, which may have, in turn, evolved into modern humans, *Homo sapiens* (Fig. 4a). Alternatively, *H. habilis* may have merely been a close relative of our ancestral lineage (Fig. 4b). More evidence will be necessary to resolve this issue. Fortunately, the fossil record has been surprisingly forthcoming with it.

Show Me the Fossils

The fossil record is, of course, incomplete, but since Darwin's time, paleontologists have discovered many, many fossils exhibiting transitional features from major milestones in the history of life. Just among the vertebrates, we have remarkably complete sets of fossils illuminating the evolution of the mammalian ear, the evolution of four-legged land dwellers from water-bound fish (e.g., Fig. 5), the evolution of whales from land mammals, the evolution of modern birds from their dinosaur ancestors, the early evolution of horses, and the early evolution of our own lineage, hominids. We probably have a more complete understanding of these major transitions than Darwin ever imagined we could—and not just because science has had 150 more years to discover new fossils.

Our improved understanding of geology, fossilization, and the history of life have provided critical information about where to look for fossils with transitional features. In fact, *Tiktaalik* was not discovered by chance but because scientists went looking for it. Previous research had suggested that vertebrates made the transition to land-living in river ecosystems about 375 million years ago—so paleontologists began their search in 375 million-year-old rocks that had preserved a river delta. When the scientists did discover *Tiktaalik*, its form was not much of a surprise: *Tiktaalik* had the set of characteristics that they had expected to find in such an organism, based on other transitional fossils.

Links in the Chain?

In his article, Tattersall also explains that the whole idea of links (missing or not) is rooted in previous concepts of the Great Chain of Being—the idea that organisms can be

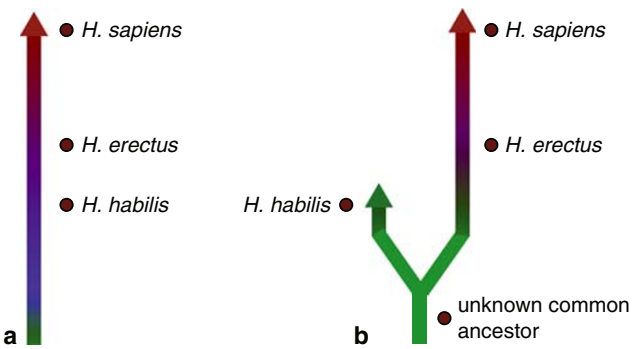

Fig. 4 Phylogenies illustrating two hypotheses regarding human ancestry. **a** According to this hypothesis, *H. habilis* is a direct ancestor of modern humans. **b** According to this hypothesis, *H. habilis* is closely related to the direct ancestor of modern humans. Illustration adapted with permission from the Understanding Evolution website

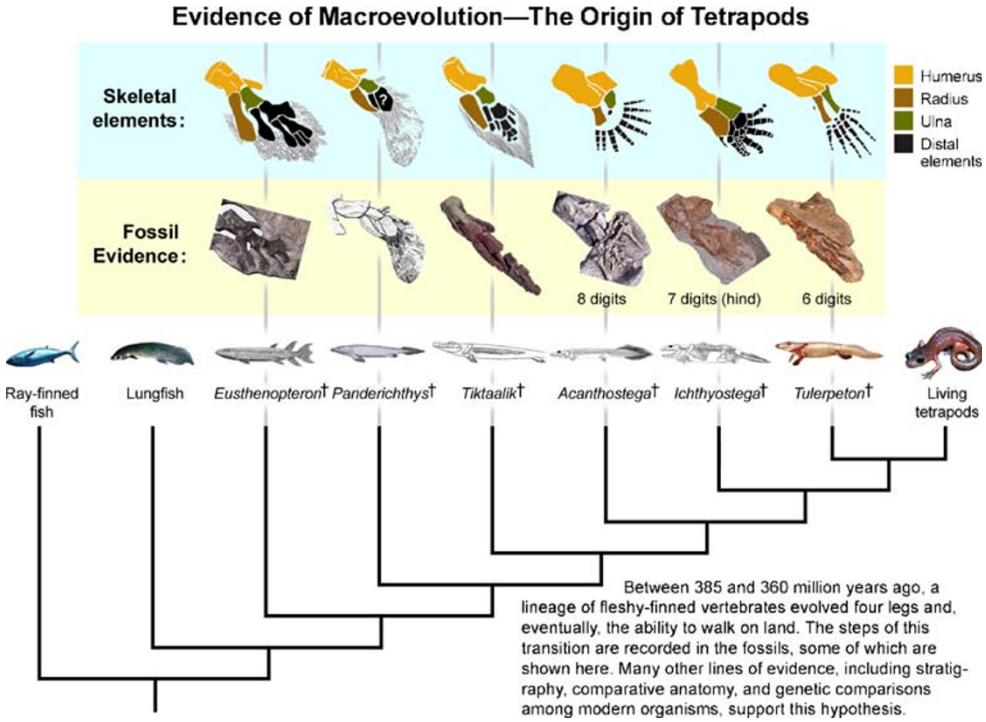

Fig. 5 Transitional fossils illustrating the evolution of the tetrapod limb. Reproduced with the permission of Kevin Padian (2008)

arranged in a sequence from lowest to highest, with humans looking down upon other species. As Tattersall notes, Darwin was not an advocate of this idea—and yet the Great Chain of Being has sometimes been twisted into an evolutionary version of the same notion. According to this view, humans are more evolutionarily advanced than other species. It is understandable why this view is attractive. Humans view the tree of life from the vantage point of our own tiny twig. We trace the hominid branch back in time—passing long-lost relatives along the way (our Neanderthal cousins, Great Aunt Lucy…)—until we reach the ancestor linking us with other primates and marvel at how far we have come.

This view manifests itself in common misconceptions—like the notion that humans evolved from chimpanzees. A glance at an evolutionary tree, however, will reveal an obvious flaw in this thinking: We humans *are* at the tip of our branch on the phylogeny, but chimpanzees are also at the tip of theirs (Fig. 6). The relationship between chimps and humans is more like that of cousins—not that of ancestor and descendent. We share a common ancestor that was neither chimpanzee nor human, and we are both linked to that ancestor by our own chains of descent, made up of organisms with transitional features.

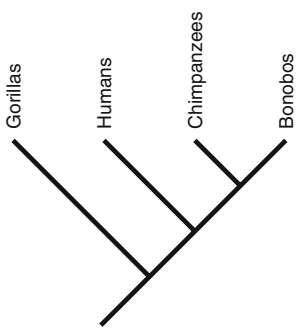

Fig. 6 Chimpanzees are the evolutionary cousins of humans—not our ancestors

By focusing on our own history, we ignore the evolutionary history of other modern lineages. Humans, chimpanzees, bonobos, bugs, and bacteria—indeed all modern forms of life—have unique evolutionary histories leading up to their modern forms. We have all retained some features that our ancestors had, and we have all evolved some new features. It is tempting to see evolution as a grand, progressive ladder with *H. sapiens* occupying the top rung. But evolution produces a tree (and a bushy one at that!), not a ladder—and we are just one of many leaves on the tree (Fig. 7).

The notion of the Great Chain of Being is invalid, but not just because modern organisms lack any sort of ancestor–descendent relationship to one another. The whole idea of ranking organisms on a grade, from primitive to advanced, implies that there is an objective way to measure advancement. But this unbiased measure simply does not exist. We humans are familiar with our own species and tend to see our own adaptations and abilities (big brain, complex culture, unusual ability to manipulate our surroundings) as unparalleled innovations. But that value judgment is unjustified. Another organism might see it differently. Imagine, for a moment, evolutionary history from the point of view of a spider. A spider might not notice any huge difference between humans and chimps. We are just a couple of hairy mammals with big heads—

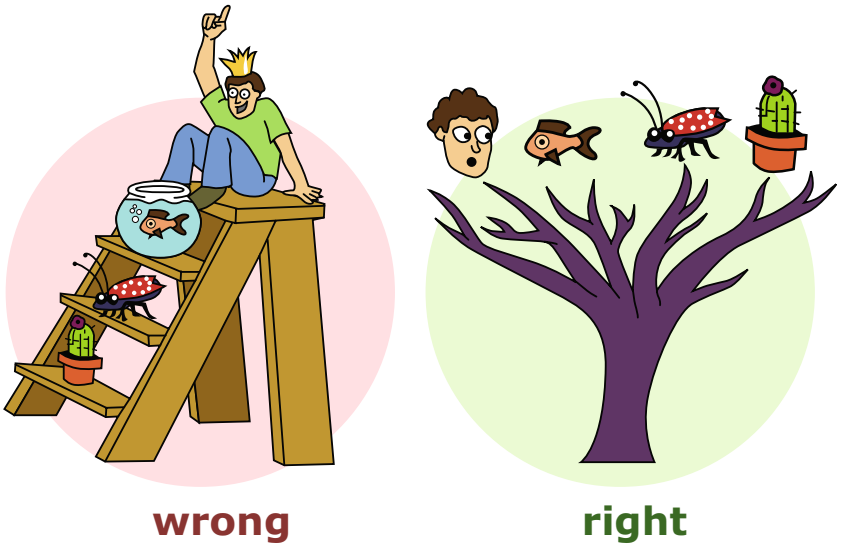

Fig. 7 Evolution produces a bushy tree, not a ladder of progress. Illustration adapted with permission from the Understanding Evolution website

and, after all, what is a little difference in brain size, compared to, say, a spider's intricate mating rituals, impressive silk-secreting apparatus, and complex web design? That spider might be just as impressed with its own evolutionary innovations as we are with our own adaptations. The same perspective-shifting exercise could be applied to any organism on the tree of life, including chimpanzees. In fact, some recent research suggests that, in some ways (namely, the adaptive evolution of proteins), chimpanzees may have evolved *more* than humans have since our two lineages split (Bakewell et al 2007). In short, as players ourselves, humans are in no position to make an objective assessment of who "wins" the evolutionary game. We are not outside or above the tree of life—but a part and product of it.

Give Me an Example of That

Check out more fossils that exhibit transitional features:

- Whale evolution. Here, we focused mainly on fossil organisms that illustrate the evolutionary steps linking fish to modern tetrapods. This video clip and short article from WGBH takes this transition full circle, exploring some of the fossil evidence that helps us understand how some land-dwelling tetrapods made their way back into the water and became whales (http://www.pbs.org/wgbh/evolution/library/03/4/l_034_05.html)

Branch Out

Many articles in this issue, including Ian Tattersall's article, explore historical perspectives on evolution. Use the following online resources to learn more about early views of evolution and fossils:

- Find out how people viewed fossils in the earliest days of paleontology in this short article from the Understanding Evolution website: http://evolution.berkeley.edu/evolibrary/article/history_04
- Find out more about science's earliest views of human evolution in this short article from the Understanding Evolution website: http://evolution.berkeley.edu/evolibrary/article/history_17

Or learn about a thoroughly modern approach to studying human evolution:

- Evolutionary biologist Leslea Hlusko's research takes her from the deserts of Ethiopia, where she hunts for hominid and primate fossils, to a baboon colony in San Antonio where she takes thousands of measurements of the primates' imposing canines. Find out how the two projects are linked, in this research profile from the Understanding Evolution website: http://evolution.berkeley.edu/evolibrary/article/hlusko_01

Dig Deeper

Visit Understanding Evolution online to find out even more about some of the examples described here:

- A news item addressing the discovery of *Tiktaalik*: http://evolution.berkeley.edu/evolibrary/news/060501_tiktaalik
- A news item describing a recent fossil discovery in the area of human evolution: http://evolution.berkeley.edu/evolibrary/news/070901_headlines

- A news item explaining research that suggests that, in some ways, chimpanzees may have evolved *more* than humans have: http://evolution.berkeley.edu/evolibrary/news/070501_chimps

In the Classroom

Numerous resources are available to introduce middle and high school students to the process of fossilization and to help them understand how scientists use the fossil record to learn more about evolution. Because many students are naturally interested in fossils and the extinct forms of life they represent, these lessons would make good starter activities for a unit that focuses on the evidence supporting evolutionary theory:

- *Adventures at Dry Creek* is an interactive web-based module from the University of California Museum of Paleontology, for grades 6–8. Students conduct a simulated field study at a fossil dig in Montana. This activity comes complete with an explanation of the standards addressed, lesson plans, discussion questions, and assessments (http://www.ucmp.berkeley.edu/education/explorations/reslab/newdc/index.html)
- *Stories From the Fossil Record* is a web-based module from the University of California Museum of Paleontology, for grades 5–9. This lesson provides students with a basic understanding of how fossils can be used to interpret the past. It comes complete with an explanation of the standards addressed, lesson plans, and assessments (http://www.ucmp.berkeley.edu/education/explorations/tours/stories/index.html)
- *Getting Into the Fossil Record* is an online, interactive module from the University of California Museum of Paleontology. It comes in two versions appropriate for grades 5–8 or 9–12. In it, students are introduced to fossils and the fossilization process by examining how fossils are formed and the factors that promote or prevent fossilization. It comes complete with an explanation of the standards addressed, lesson plans, and assessments (http://www.ucmp.berkeley.edu/education/explorations/tours/fossil/index.html)

Older students can extend this basic knowledge and learn more about the relationship between ancestors and descendents, as well as the fossil features that help us understand those transitions. You might want to try out the following lessons:

- *The Evolution of Flight in Birds* is an online, interactive module from the University of California Museum of Paleontology, for grades 9–12. Students examine evidence from the fossil record, behavior, biomechanics, and cladistic analysis to interpret the sequence of events that led to flight in the dinosaur lineage. This module comes complete with an explanation of the standards addressed, lesson plans, and assessments (http://www.ucmp.berkeley.edu/education/explorations/reslab/flight/main.htm)
- *Hominid Cranium Comparison* is a lesson from the Evolution and the Nature of Science Institute, for grades 9–12. Students describe, measure, and compare cranial casts from contemporary apes, modern humans, and fossil hominids to discover some of the similarities and differences between these forms and to see the pattern leading to modern humans (http://www.indiana.edu/~ensiweb/lessons/hom.cran.html)

Older students may have developed misconceptions about some of the key concepts addressed in this article. You can deal with these directly using lessons like this one:

- *Investigating Common Descent: Formulating Explanations and Models* is a lesson from the National Academy of Sciences, for grades 9–12. Students formulate explanations and models that simulate structural and biochemical data as they investigate the misconception that humans evolved from apes (http://www.nap.edu/openbook.php?record_id=5787&page=81)

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