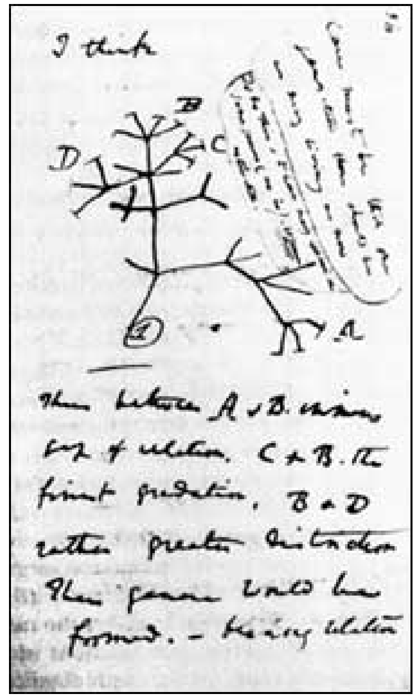
The big issues

All available evidence supports the central conclusions of evolutionary theory, that life on Earth has evolved and that species share common ancestors. Biologists are not arguing about these conclusions. But they are trying to figure out how evolution happens, and that's not an easy job. It involves collecting data, proposing hypotheses, creating models, and evaluating other scientists' work. These are all activities that we can, and should, hold up to our checklist and ask the question: are they doing science?

All sciences ask questions about the natural world, propose explanations in terms of natural processes, and evaluate these explanations using evidence from the natural world. Evolutionary biology is no exception. Darwin's basic conception of evolutionary change and diversification (illustrated with a page from his notebook at right) explains many observations in terms of natural processes and is supported by evidence from the natural world.



A page from Darwin's notebook.
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Some of the questions that evolutionary biologists are trying to answer include:

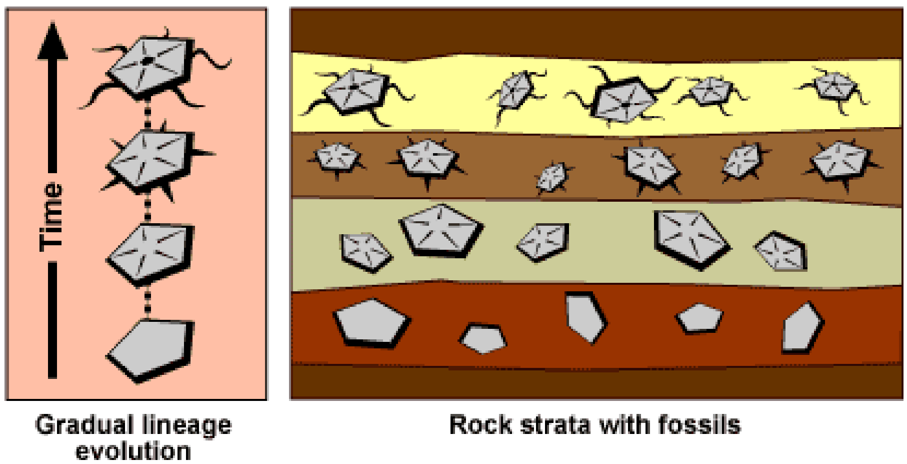
1. Does evolution tend to proceed slowly and steadily or in quick jumps?
2. Why are some clades very diverse and some unusually sparse?
3. How does evolution produce new and complex features?
4. Are there trends in evolution, and if so, what processes generate them?

The pace of evolution

Does evolution occur in rapid bursts or gradually? This question is difficult to answer because we can't replay the past with a stopwatch in hand. However, we can try to figure out what patterns we'd expect to observe in the fossil record if evolution did happen in bursts, or if evolution happened gradually. Then we can check these predictions against what we observe.

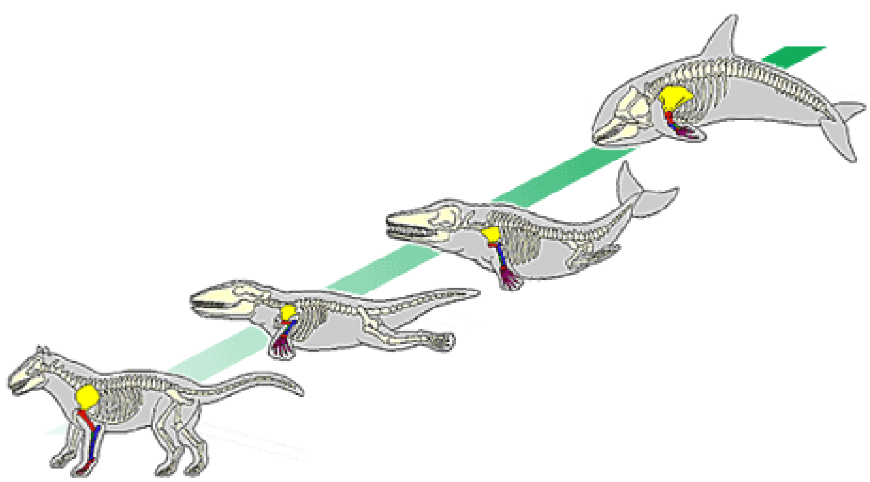
What should we observe in the fossil record if evolution is slow and steady?

If evolution is slow and steady, we'd expect to see the entire transition, from ancestor to descendant, displayed as transitional forms over a long period of time in the fossil record.



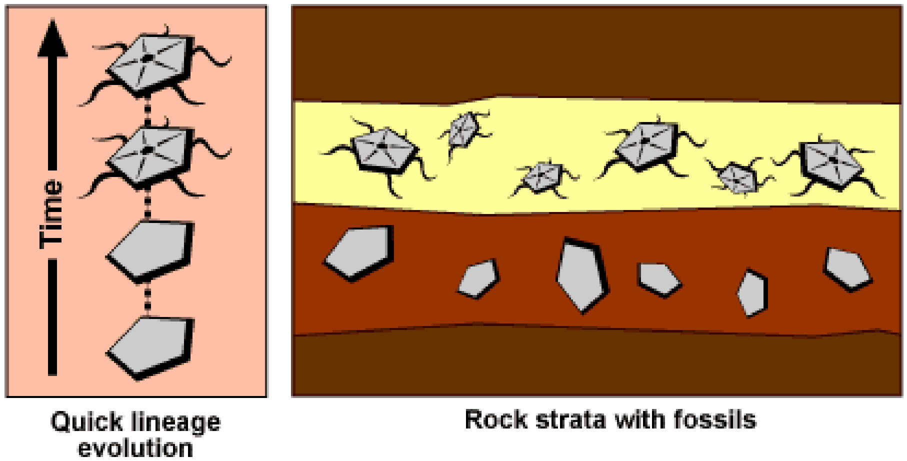
In the above example, the preservation of many transitional forms, through layers representing a length of time, gives a complete record of slow and steady evolution.

In fact, we see many examples of transitional forms in the fossil record. For example, to the right we show just a few steps in the evolution of whales from land-dwelling mammals, highlighting the transition of the walking forelimb to the flipper.



Transitional forms in whale evolution.

What would we observe in the fossil record if evolution happens in "quick" jumps (perhaps fewer than 100,000 years for significant change)? If evolution happens in "quick" jumps, we'd expect to see big changes happen quickly in the fossil record, with little transition between ancestor and descendant.

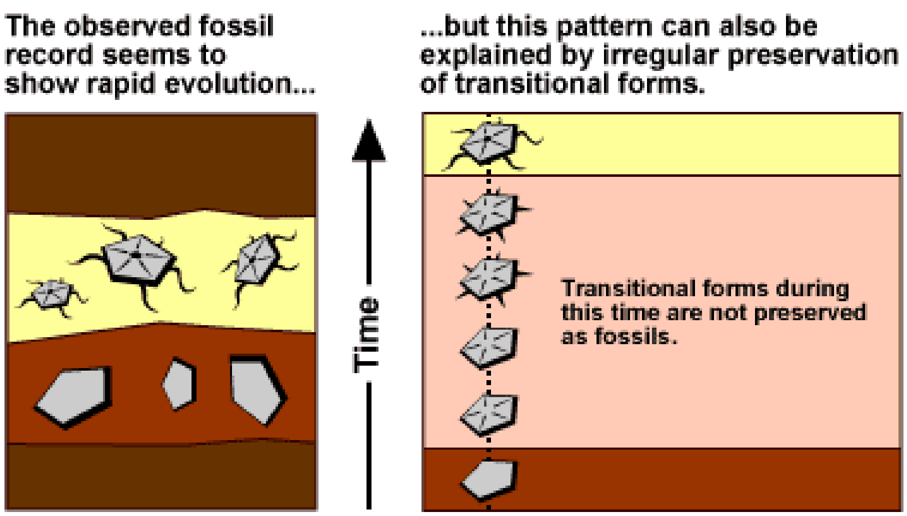


In the above example, we see the descendant preserved in a layer directly after the ancestor, showing a big change in a short time, with no transitional forms.

When evolution is rapid, transitional forms may not be preserved, even if fossils are laid down at regular intervals. We see many examples of this "quick" jumps pattern in the fossil record.

Does a jump in the fossil record necessarily mean that evolution has happened in a "quick" jump?

We expect to see a jump in the fossil record if evolution has occurred as a "quick" jump, but a jump in the fossil record can also be explained by irregular fossil preservation.



This possibility can make it difficult to conclude that evolution has happened rapidly.

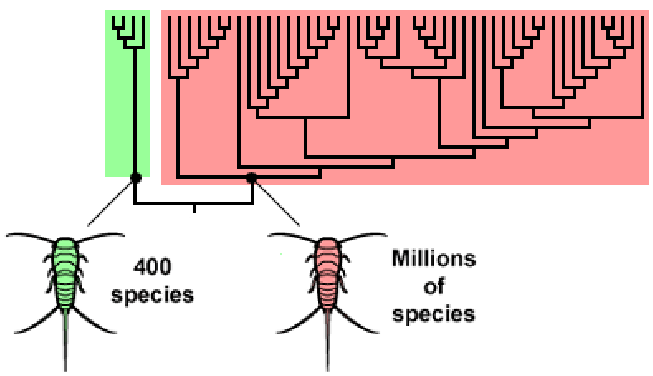
We observe examples of both slow, steady change and rapid, periodic change in the fossil record. Both happen. But scientists are trying to determine which pace is more typical of evolution and how each sort of evolutionary change happens.

Diversity in clades

Imagine that you've traveled back in time to around 350 million years ago, give or take 50 million years. Your goal is to check out the cool insects living at this point in time. You see a lot of little insects that look like modern silverfish — no big deal.Imagine that you've traveled back in time to around 350 million years ago, give or take 50 million years. Your goal is to check out the cool insects living at this point in time. You see a lot of little insects that look like modern silverfish — no big deal.

Silverfish photo courtesy of T.W. Davies © California Academy of Sciences.

But something interesting and significant is happening that you can't see — a lineage has split into two. One of these newly isolated lineages will eventually give rise to about 400 extant species that look a lot like the ancient insects you see. But the other lineage will give rise to millions of extant insect species, the bulk of animal life on Earth today. Why is there such a big difference in diversity between these two lineages? After all, they were indistinguishable 350 million years ago…

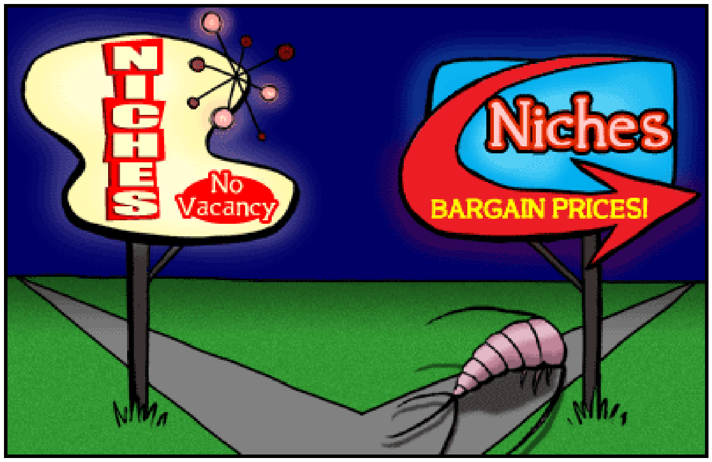


Why would one lineage lead to millions of species and the other to only 400?

1. **Opportunity knocks:** One possibility is that the now-diverse lineage happened to be in the right place at the right time. The environment presented opportunities, and the lineage was able to take advantage of them. What sorts of factors in the environment might encourage diversification?

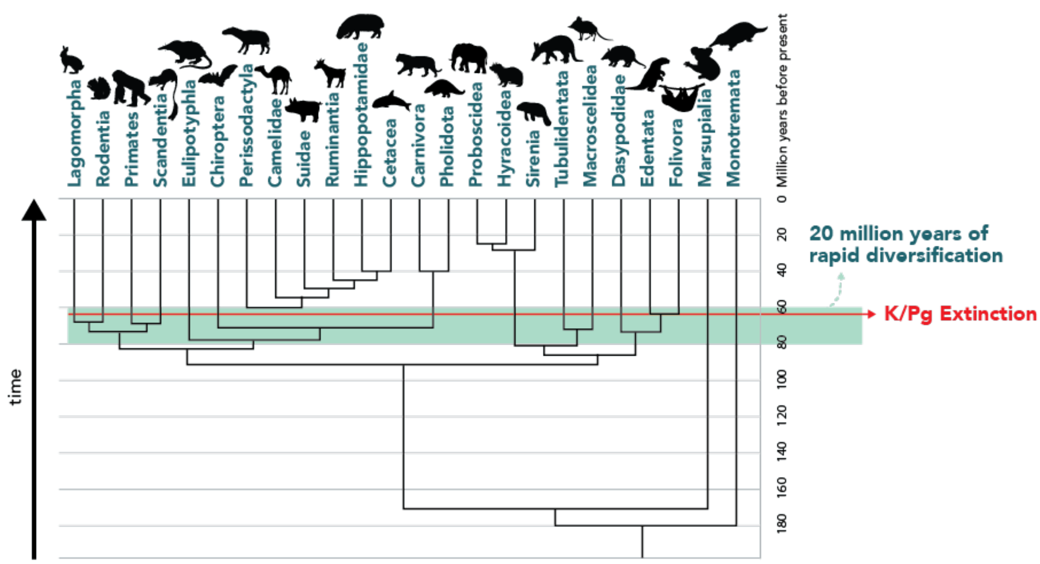
   - The environment may have offered opportunities for specialization.
   - A fragmented environment might make reproductive isolation likely.
   - The environment may have provided a release from competition with other insects.

   All of these factors might be at work in some situations. Consider a plant-eating insect that colonizes a tropical island. On its mainland home, the insect's population size and range of resources is constrained by other species competing for the same resources. But the lack of similar species on the island means open niches and reduced competition from other species. Further, the island offers new kinds of food in the form of plants that the insect has never seen before. Selection might allow some insects to specialize on these new plants. Hanging around each kind of plant might mean that the insects get to mate with insects on a different plant less frequently, encouraging reproductive isolation. All of these factors can drive diversification — *but only* if the population has the genetic variation to take advantage of the opportunities presented by the environment.



Being in the right place at the right time is a reason that one clade might be more diverse than another.

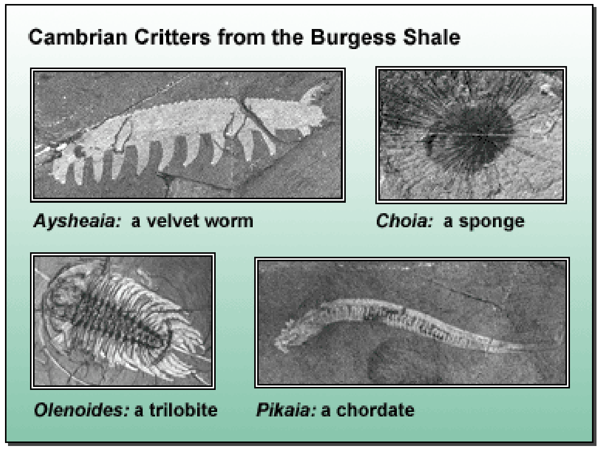
2. **Adaptive Radiation:** If all of this diversification happens in a short amount of time, it is often referred to as an adaptive radiation. Although biologists have different standards for defining an adaptive radiation, it generally means an event in which a lineage rapidly diversifies, with the newly formed lineages evolving different adaptations. The rapid diversification of mammals shown below may constitute an adaptive radiation.



Tree adapted from Upham, N.S., Esselstyn, J.A., Jetz, W., 2019. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biol 17, e3000494. https://doi.org/10.1371/journal.pbio.3000494 Tree adapted from Upham, N.S., Esselstyn, J.A., Jetz, W., 2019. Inferring the mammal tree: Species-level sets of phylogenies for questions in ecology, evolution, and conservation. PLoS Biol 17, e3000494. https://doi.org/10.1371/journal.pbio.3000494

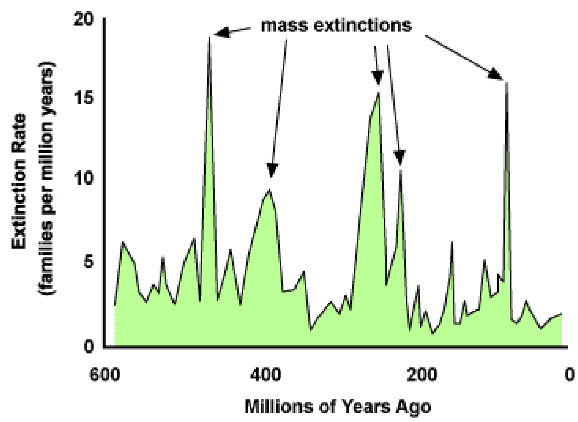
3. **Historical changes in diversity:** Many events have left their marks on the diversity of life on Earth, pruning or growing the tree of life, but a few stand out as unusually important:

a. **Explosion:** About 530 million years ago, a huge variety of marine animals suddenly burst onto the evolutionary scene. (Of course, "suddenly," in geological terms, means in perhaps 10 million years). These animals had a variety of new body forms that evolution has been using to produce "spin-offs" ever since, such as these representatives from the Burgess Shale.



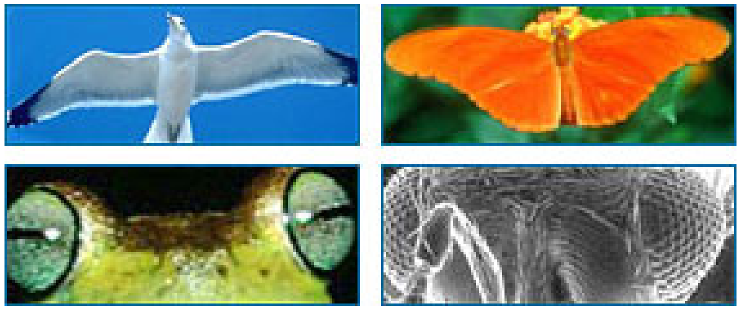
Images courtesy of Chip Clark, Museum of Natural History, Smithsonian Institution.

b. **Extinction:** About 225 million years ago, over 90% of the species alive at the time went extinct in fewer than 10 million years. Some groups that were dominant before the extinction never recovered. The cause of this extinction is the subject of much debate, but of equal significance is that it set the stage for a massive diversification of taxa that filled the empty niches.



Looking at complexity

Life is full of grand complications, such as aerodynamic wings, multi-part organs like eyes, and intricate chemical pathways. When faced with such complexity, both opponents and proponents of evolution, Darwin included, have asked the question: how could it evolve?



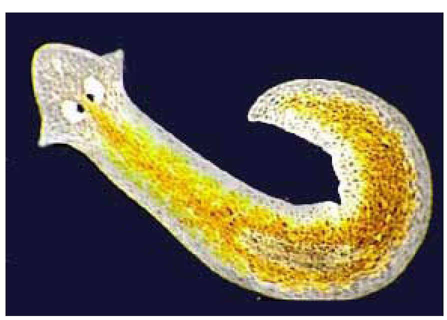
Complex adaptions: bird wings, insect wings, vertebrate eyes, and insect eyes. Gull photo courtesy of Dr. Lloyd Glenn Ingles © California Academy of Sciences; Butterfly photo © 2002 John White; Insect microscopy courtesy of Electron Microscope Lab UC Berkeley; Tree frog photo © 2003 Twan Leenders.

Science does not sweep such difficult questions under the rug, but takes them up as interesting areas for research. The difficulty is as follows.

Since many of these complex traits seem to be adaptive, they are likely to have evolved in small steps through natural selection. That is, intermediate forms of the adaptation must have evolved before evolution arrived at a fully-fledged wing, chemical pathway, or eye. But what good is half a wing or only a few of the elements of an eyeball? The intermediate forms of these adaptations may not seem adaptive — so how could they be produced by natural selection?

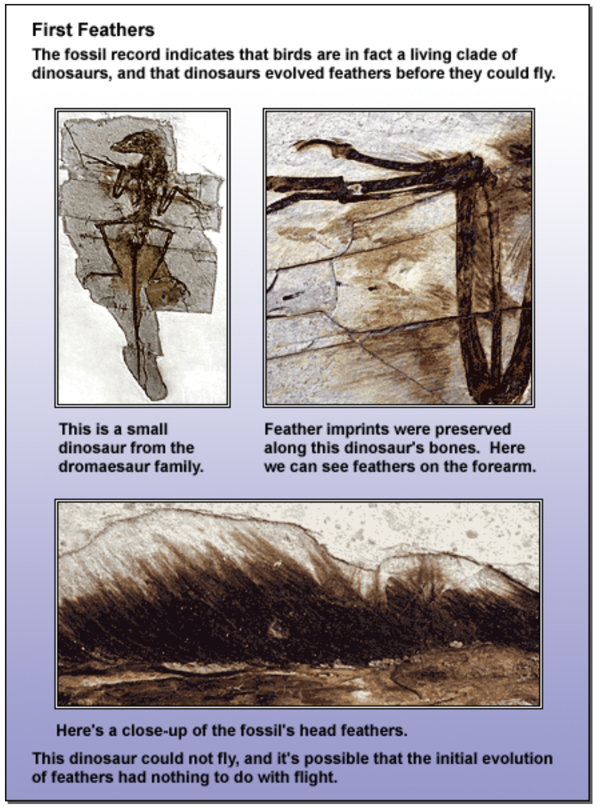
There are several ways such complex novelties may evolve:

- **Advantageous intermediates:** It's possible that those intermediate stages actually were advantageous, even if not in an obvious way. What good is "half an eye?" A simple eye with just a few of the components of a complex eye could still sense light and dark, like eyespots on simple flatworms do. This ability might have been advantageous for an organism with no vision at all and could have evolved through natural selection.



A Planaria flatworm with its light-sensitive eyespots. Photo courtesy of BioMEDIA ASSOCIATES.

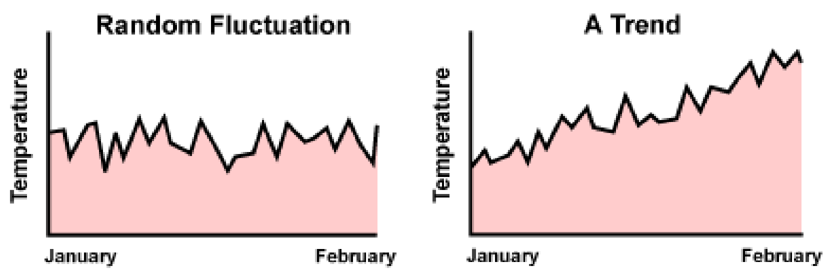
- **Co-opting:** The intermediate stages of a complex feature might have served a different purpose than the fully-fledged adaptation serves. What good is "half a wing?" Even if it's not good for flying, it might be good for something else. The evolution of the very first feathers might have had nothing to do with flight and everything to do with insulation or display. Natural selection is an excellent thief, taking features that evolved in one context and using them for new functions.



Photos courtesy of Mick Ellison, AMNH.

Trends in Evolution

An evolutionary trend can be either directional change within a single lineage or parallel change across lineages, in other words, several lineages undergoing the same sort of change. However, not just any change counts as a trend. After all, if the weather gets warmer one day, you wouldn't call it a warming trend; warming would have to go on for some length of time before you'd call it a trend. Biologists think about evolutionary trends in the same way — there has to be something about the change that suggests that it's not just a random fluctuation before it counts as a "trend."



For example, titanotheres (a cool, extinct clade related to modern horses and rhinos) exhibit an evolutionary trend. Titanotheres had bony protuberances extending from their noses. The sequence of fossil skulls from these animals shows that evolutionary changes in the size of these "horns" were not random; instead, changes were biased in the direction of increasing horn size. And in fact, several different titanothere lineages experienced the same sort of change in horn size.

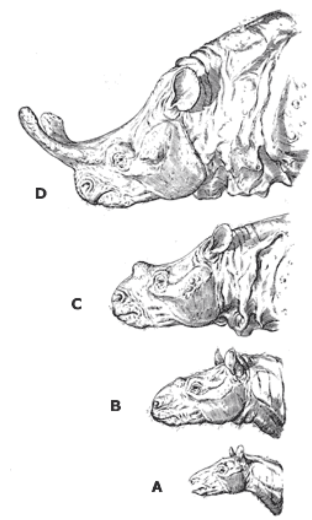


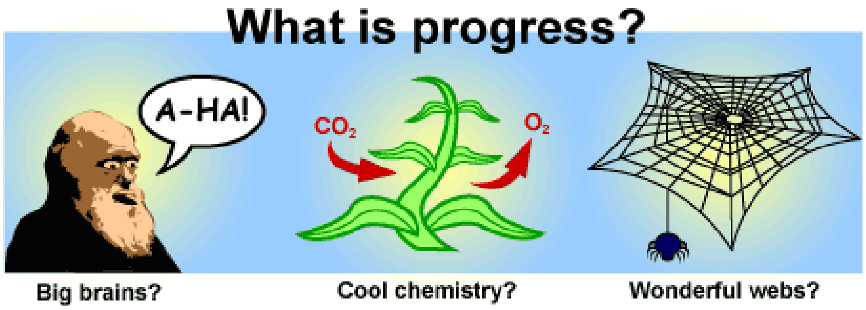
Illustration from Osborn, H.F. 1929 The titanotheres of ancient Wyoming, Dakota and Nebraska. U.S. Geol. Surv. Monogr. 55.

The titanothere reconstructions shown here range from about 55 mya (A) to 35 mya (D).The cause of this trend is not obvious. It may be a by-product of selection for increasing body size, and/or it may be a result of selection on horn size directly: big-horned individuals may have had an advantage in "butting" contests for females, as in sheep and goats.

Other evolutionary trends are not consistent across lineages. For example, biologists have long investigated whether there is a trend towards the evolution of larger body sizes. Since life started out so small, average body size has, of course, gone up over the course of life's history. There was no direction to go but bigger! And of course, many lineages have remained microscopic throughout 3.5 billion years of evolutionary history. Some groups of macroscopic organisms (like non-avian dinosaurs and marine species) *do* seem to have evolved larger and larger body sizes over time. But there are also many examples of lineages that show no particular trend at all (e.g., horses) or seem to evolve smaller body sizes than their ancestors – for example, in cases of island-dwelling and parasitic lineages.

Is evolution progressive?

This is not an easy question to answer. From a plant's perspective, the best measure of progress might be photosynthetic ability; from a spider's it might be the efficiency of a venom delivery system.



The problem is that we humans are hung up on ourselves. We often define progress in a way that hinges on our view of ourselves, a way that relies on intellect, culture, or emotion. But that definition is anthropocentric.

It is tempting to see evolution as a grand progressive ladder with *Homo sapiens* emerging at the top. But evolution produces a tree, not a ladder — and we are just one of many leaves on the tree.