

Biology 1B—Evolution Lecture 11,

- Interactions between diverging lineages: Secondary contact
- Insights from the Fossil Record – timing of events and extinction

What happens when two independently evolving lineages meet? When two lineages that evolved from a single ancestral population encounter each other once again, it is called secondary contact. There are several possible outcomes on secondary contact:

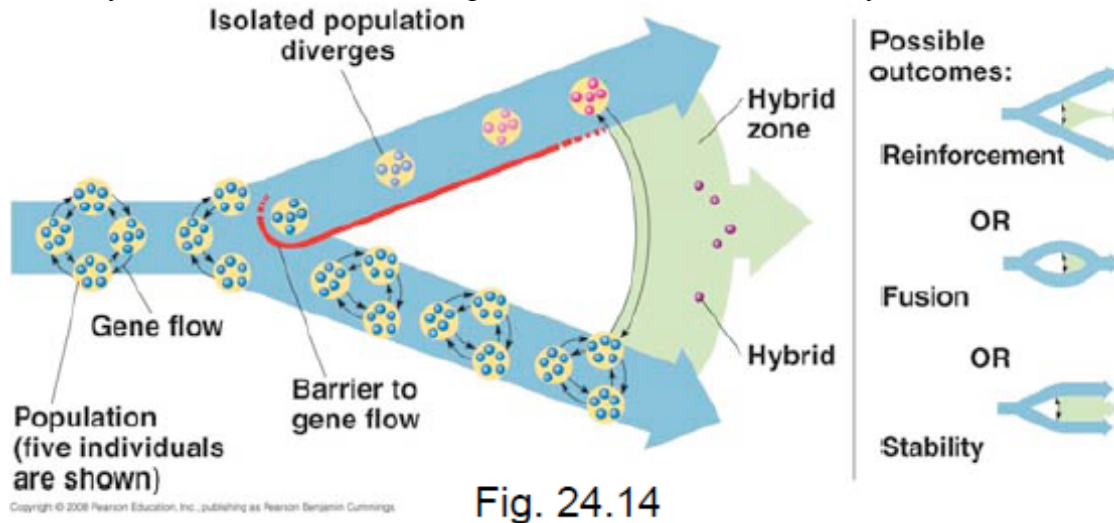


Figure 2: Possibilities of secondary contact: reinforcement, fusion, stable hybrid zone
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Figure 3: possibilities of secondary contact: Hybrid Speciation
Christopher Pavia, 2009.

1. No **hybridization** occurs; if these two lineages occupy different ecological niches and can exist sympatrically (in the same environment) they are “good species” by any criterion.
2. **Fusion**: members of the two lineages mate together, forming hybrids with normal fitness, and eventually collapse into one species. Note that since independent evolution has been occurring while the two populations were separate, resulting in a lineage that will not be identical to the ancestral lineage. Typically this new lineage will be regarded as the same species, however.
3. Stable **hybrid zone**: each lineage maintains its own range separate of each other save for some areas of overlap. In those regions, the hybrids have

reduced fitness and the hybrid zone is maintained by immigration from adjacent parent populations. [e.g. Bombina frogs in central Europe]

4. **Reinforcement:** selective pressure to avoid mating (hybrids are either inviable or infertile) will eventually lead to choice #1. Examples include a frog hybrid zone in the Australian rainforest & others in the Hillis et al. text.
5. **Hybrid speciation:** formation of a 3rd species (lineage) if the hybrids are normal fertility & viability and are somehow isolated from both of the parental lineages. For example, consider plant hybrids and polyploidy, also known as “allopolyploidy.” in this case, the new hybrid taxon has another set of chromosomes (e.g. 4N) and hybrids with their parental species (4N x 2N = 3N) will be sterile.

Fossil Record

Microevolution $\xrightarrow{\text{(speciation)}}$ Macroevolution

The **fossil record** is our primary source of information on the past, including the timing of various extinction and evolutionary events and the phenotypes of ancestral forms. Sedimentary rocks created by erosion (often in a marine environment) form strata, with different layers corresponding to different time periods. Consider the Grand Canyon, formed by the Colorado River over 20 million years: the exposed strata, from the top of nearby Bryce Canyon to the bottom of the Grand Canyon itself, cover the last billion years. These layers can be dated by analyzing proportions of different isotopes present in each of the strata.

Fossils provided both key evidence and frustration to Darwin when writing *the Origin of the Species*. Fossils showed there were many creatures which no longer existed; but these animals existed at some point, and must have been adapted to the environment in which they lived. This further reinforced the idea that the present and past are ruled by the same physical processes. However, it was frustrating in that many complex creatures seemed to suddenly appear in the fossil record, without preceding transitional forms. Darwin predicted that these gaps would be filled, and many of the gaps he predicted have now been filled.

Some major transitions in earth history

	Billions of Years Ago
Earth and Solar System formation	4.5
Earliest prokaryote fossils	3.5
Increase in oxygen – implies photosynthesis	2.7
Single-celled fossil eukaryotes	2.1-1.2
Complex metazoan (multi-celled animals)	0.5
Hominids (apes and humans)	0.005

The Cambrian Explosion is a time period from 550 million years ago (appearance of complex metazoans) when many species and new body forms appear in the fossil record. The fossils preceding that 550 million years ago mark are very scarce, then suddenly there is a large diversity of fossils and body forms.

What caused this diversity? There are several possibilities. Firstly, perhaps before the Cambrian period, all organisms were soft-bodied, and thus did not mineralize and leave behind fossils. Supporting this hypothesis is that scientists have discovered fossil impressions of organisms older than the Cambrian period. Another possibility is that the rapid appearance of new species was due to an evolutionary innovation allowing the rapid diversification of body forms that did not exist before. Yet another is that the concentration of atmospheric oxygen, increasing via photosynthesis, reached a threshold level that permitted evolution of multicellular (“metazoan”) animals

The **Burgess Shale** is a site in Canada excavated by Charles Walcott that has yielded many excellent Cambrian fossils, including forms of arthropods with no modern counterparts.

Extinction

Now, consider fossils in tandem with extinction. Extinction is normal enough: 97% of all species ever extant on Earth are now extinct. We can determine extinction rates by following species that fossilize well through the various rock strata. Eventually, having gone extinct, they stop appearing in the fossil record. The background rate of extinction for marine invertebrates is less than 0.1 extinction per million species per year; or in the following graph, about 3-4 families per MY. However, there are some large peaks in the extinction rates which we call **mass extinctions**, defined as having >75% species extinct within a million years. Two major extinctions we will explore further are the **Permian-Triassic** extinction (250mya) and the **Cretaceous/Paleogene (k/t)** extinction (65mya), the second of which pushed the terrestrial dinosaurs into extinction and led to adaptive radiation of mammals and birds (= surviving lineage of theropod dinosaurs).

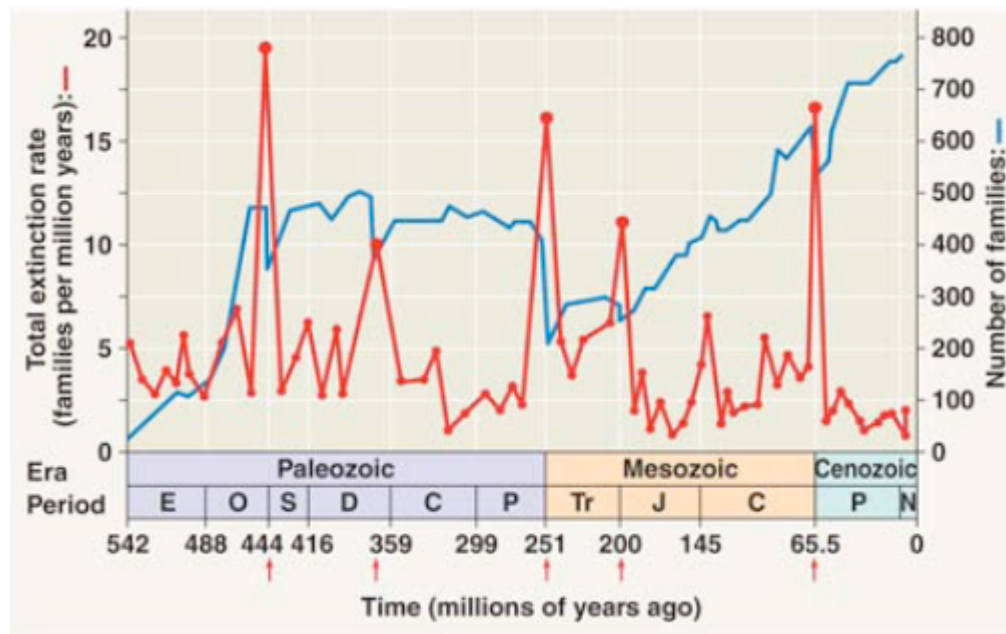


Figure 4: Graph of extinction rates over time, showing mass extinction events.

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Extinction

Important points on extinction rates:

- Background rate of extinctions per million species per year:
About 0.1 extinction per million species of marine invertebrate per year, so if there are roughly 10 million species on the planet, that would imply that about 1 species extinct per year

- Environmental pressures, such as changing temperatures or volcanism, commonly cause extinction of species, but extinction also occurs in a “constant” environment
- Broadly, a typical species lasts 2-10 million years

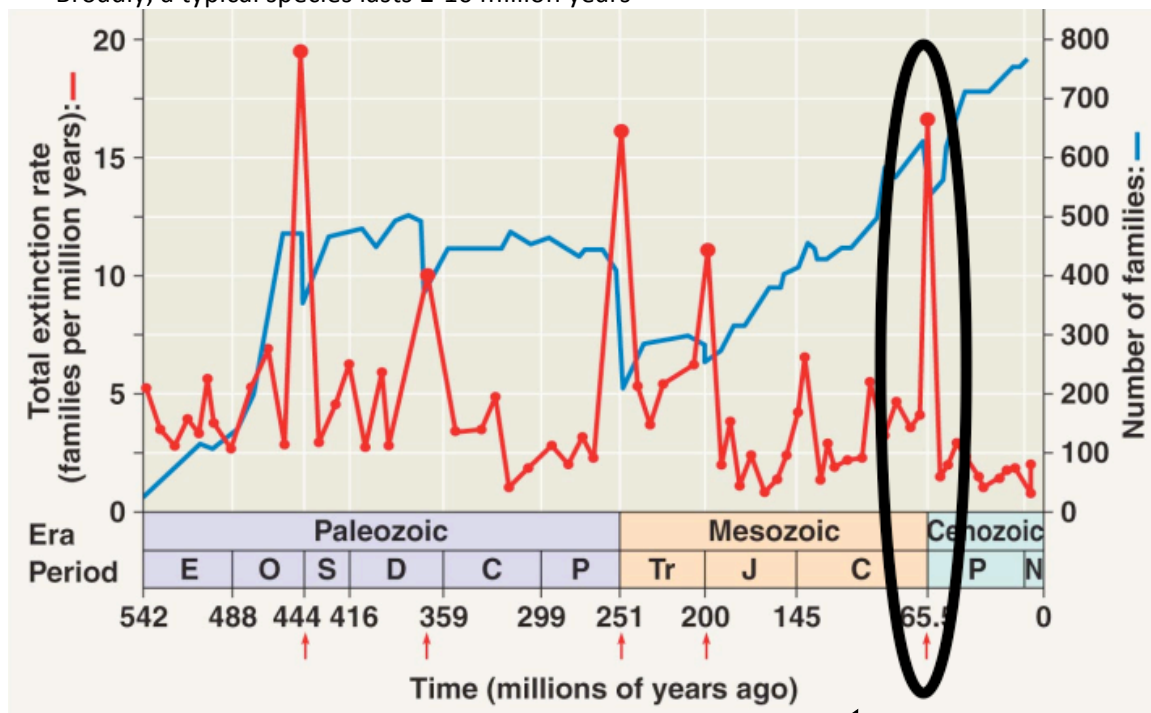
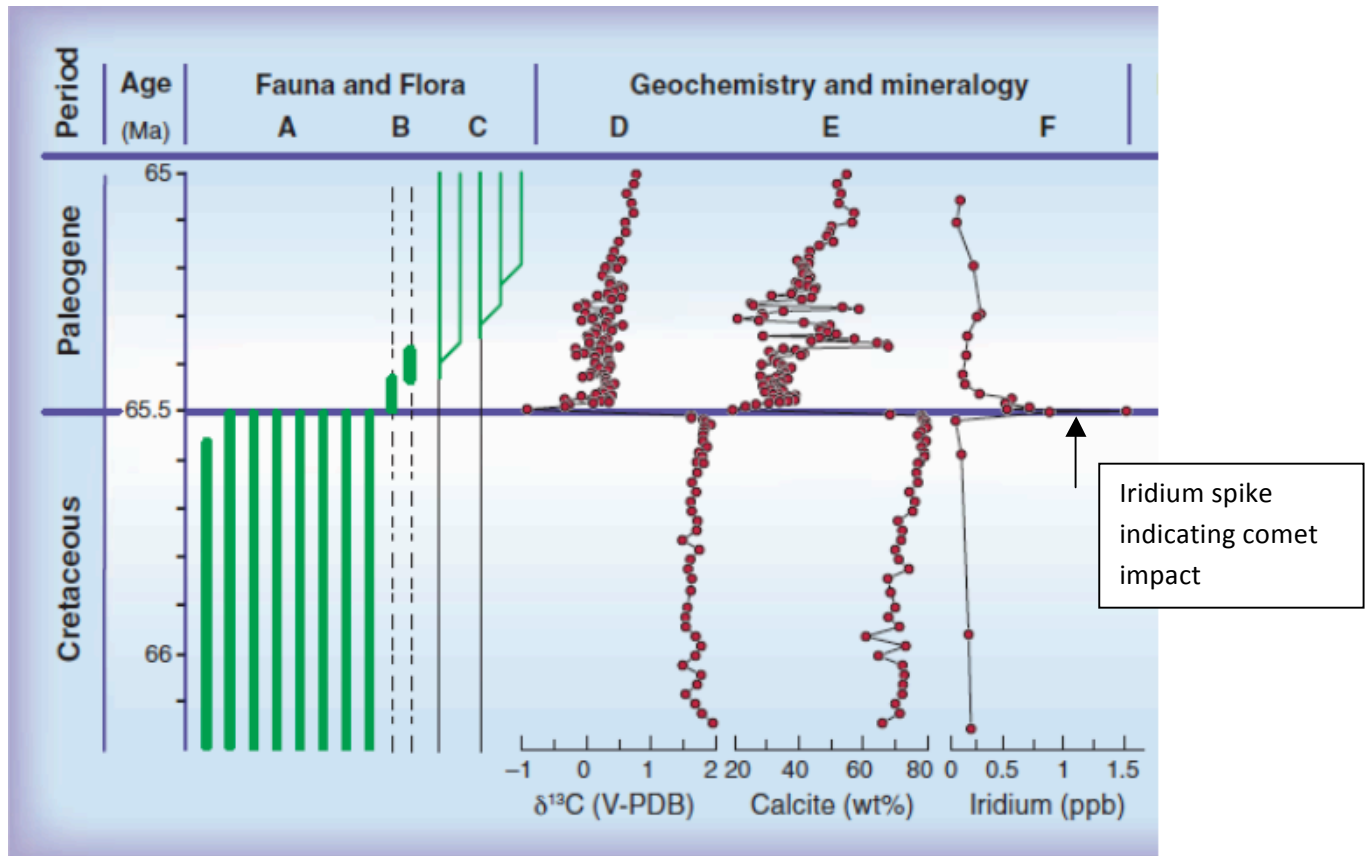


Figure 25.14 (page 521, 8th edition)

Huge extinction the result of a comet impact (more below)

Cretaceous-Paleogene (Tertiary) Extinction—K/T Boundary

- Most importantly, this marked the demise of the terrestrial dinosaurs (save for modern dinosaurs, which are birds)
- With the end of the dinosaurs came the adaptive radiation of the mammals
- Luis and Walter Alvarez (of UC Berkeley!) worked to find what caused the K/T boundary/extinction of the dinosaurs
 - Walter, a paleontologist, noticed a layer of dark silt between fossils of organisms between the Cretaceous (large-bodied animals) and Paleogene (smaller-bodied animals)
 - He asked his father, a physicist, what might be studied in the isotopes in the dark silt layer
 - They found a huge spike in the amount of iridium, which suggested a comet impact



--Despite the scrutiny and disbelief of the scientific community, the crater the comet would have left in the Yucatan was eventually found

- The massive impact of the comet ejected sediments into the air, halting photosynthesis and changing the carbon cycle of the planet
- It took about 10,000 years to restore the Earth's normal ecological processes and millions to restore diversity

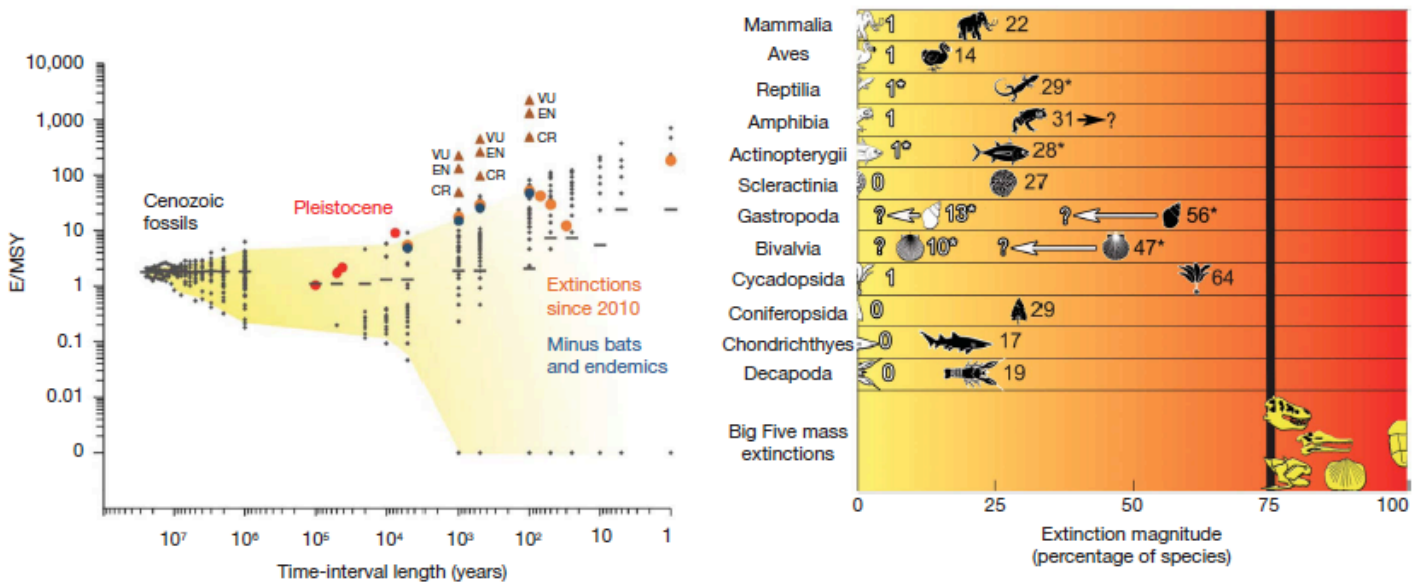
Are we causing a sixth mass extinction?

- Very difficult to know for sure, as we don't even know how many species there are on the planet (we've only described 1.6 million of perhaps 10-15 million total species). Estimates of the rate of extinction are vary according to time interval over which extinction is measured – estimates spanning >1M years of the fossil record tend to be lower (about 1 extinction per million species per year for terrestrial mammals) and more precise than rated measured over a small time span (e.g the last 100 years).
- Amphibians are closely tied to environmental conditions, and 30% of known species are now endangered
- Better evidence of a mass extinction might come from the loss of megafauna (smilodons, mastodons) that might be the result of humans hunting, climate change, or both
 - North American and Australian megafauna went extinct roughly after humans arrived in North America

Biology 1B – Evolution Lecture 12 – extinction, species selection (macroevol), transitional forms, intro to hominid evolution

--Africa still has many megafauna, suggesting that they evolved with the humans and human ancestors there

- We also see extinctions of large birds, such as rails and moas soon after the recent colonization of Pacific Islands by humans
- A recent reassessment by Tony Barnosky and grad students in IB suggests that we are not yet in a human-caused mass extinction, but extinction rates are elevated and this could lead to a mass extinction if currently threatened (Endangered & Vulnerable) species go extinct and this rate of loss is maintained for several hundred years.



Species selection

Traits that arise via microevolution can also act to increase net speciation rate (= Speciation rate – Extinction rate). Traits that increase speciation rate and/or decrease extinction rate in a clade of species can be identified through comparison of closely related clades, especially if trait arises repeatedly and is consistently associated with high species diversity in those clades relative to sister clades that lack this trait (see Figure from Rabosky & McCune 2010).

The power of species selection, relative to individual-based selection within species, is clearest when traits that are disadvantageous within species are associated with increased net speciation among clades – ie. opposing effects.

Example – evolution of self-compatibility (SC; ability to self-fertilize) in monoecious plants vs, self-incompatibility (SI, no self fertilization). SI can be a disadvantage within species if pollinators are limiting

- in this circumstance, SC allows reproduction. But in the longer-term SC increased rate of inbreeding, loss of genetic diversity etc => higher extinction rates. SC has arisen repeatedly in flowering plants (eg. Figure for Solanaceae (tomatoes & relatives)), but analysis of phylogenies suggest that it leads to higher extinction rates of species, despite short-term advantage to individuals. Thus, clades with SI have more species surviving than those with SC.

The fossil record: transitional forms

Comparison of extant (living forms) => predictions of evolutionarily transitional phenotypes in the fossil record

Major Transitions in Phenotypes

e.g. Vertebrate Fish → Amphibian Tetrapods

[see next page]

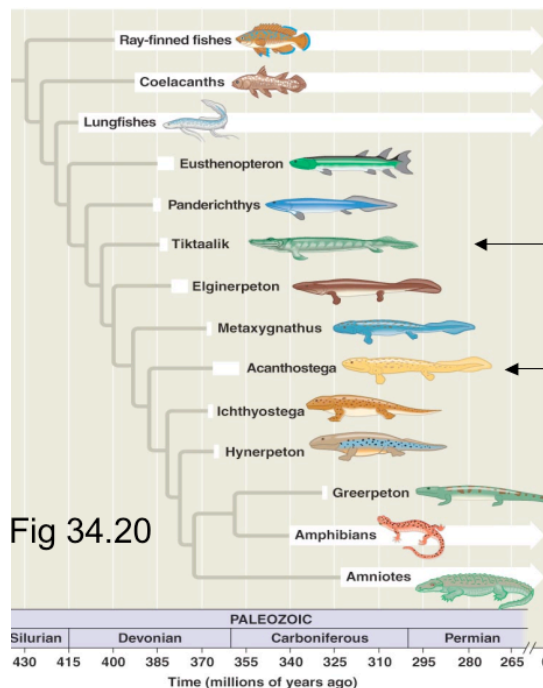
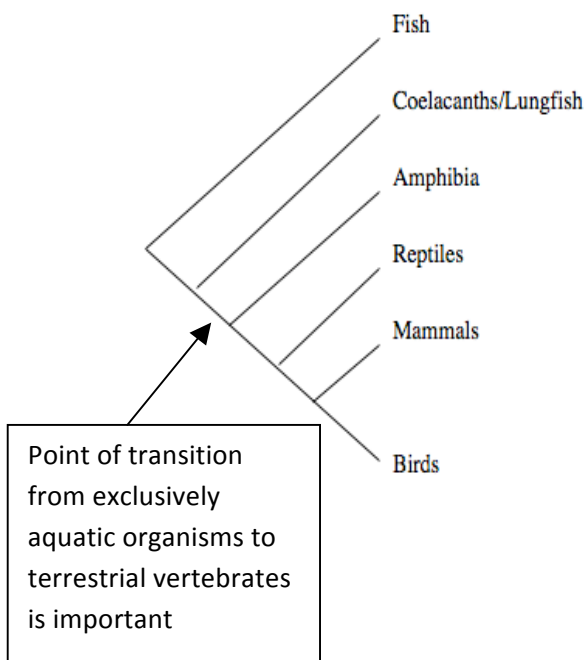


Figure 34.20 (page 711, 8th edition)

Biology 1B – Evolution Lecture 12 – extinction, species selection (macroevol), transitional forms, intro to hominid evolution

- There is a huge jump between these groups (particularly in phenotypes), which cannot be constructed from modern fauna—this is where the fossil record comes into play
- The transition from ancestors of lungfish to ancestors of tetrapods, and key insights are coming from fossils
 - Acanthostega has a moving neck, lungs, limbs, but no wrists and a weak rib cage that would have made breathing on land very difficult, so it probably lived in a swamp
 - Tiktaalik, however, has the evolved traits of Acanthostega plus wrists and a stronger rib cage (see image below)
- The extinct forms are not necessarily direct ancestors, but they do allow us to see how and when certain traits/adaptations evolved

Evolution of Novel Structures - Exaptation

- Co-opting structures from one function to another is known as **exaptation** (don't need a new structure to arise, can simply modify an existing one)
- Feathers are an example as they are present in non-flying dinosaurs – the ancestors of modern (flying) birds—their original purpose may not have been for flight, but rather for attracting mates or thermoregulation
 - new studies have found dinosaurs with feathers that were colored, but not for flight, suggesting their use in display

Evolution of Homo and related hominids

Family Hominidae = monophyletic group consisting of modern humans, chimpanzees, gorillas, orangutans (the “great apes”) and species now extinct within each of these lineages.

Subfamily Homininae = monophyletic group consisting of humans and ancestral, now extinct taxa (e.g. including members of the genera *Homo*, *Australopithecus*, *Paranthropus* and *Ardipithecus*) back to the common ancestor with the chimpanzee lineage.

Early applications of the molecular clock (by Sarich and Wilson at UC Berkeley) suggest the split between the lineages leading to living chimpanzees on one branch and humans on the other occurred about 7 million years (mya) ago: the last common ancestor between chimpanzees and humans existed around 7mya. Therefore, humans are **not** descended from chimpanzees: the chimpanzee lineage has been evolving independently as long as our lineage has. Our common ancestor did not look like either chimpanzees or humans: for example, consider *Ardepithecus ramidus* from 4mya (discovered by Tim White, and visible in the display outside the Marian Koshland Biosciences Library). It is our ancestor, yet it does not look like us. It is neither a chimpanzee nor a human.

When looking at the graph below, note that it is not a phylogeny or even a cladogram: there is still much debate on the phylogeny and even the taxonomy of these different species.

Biology 1B – Evolution Lecture 12 – extinction, species selection (macroevol), transitional forms, intro to hominid evolution

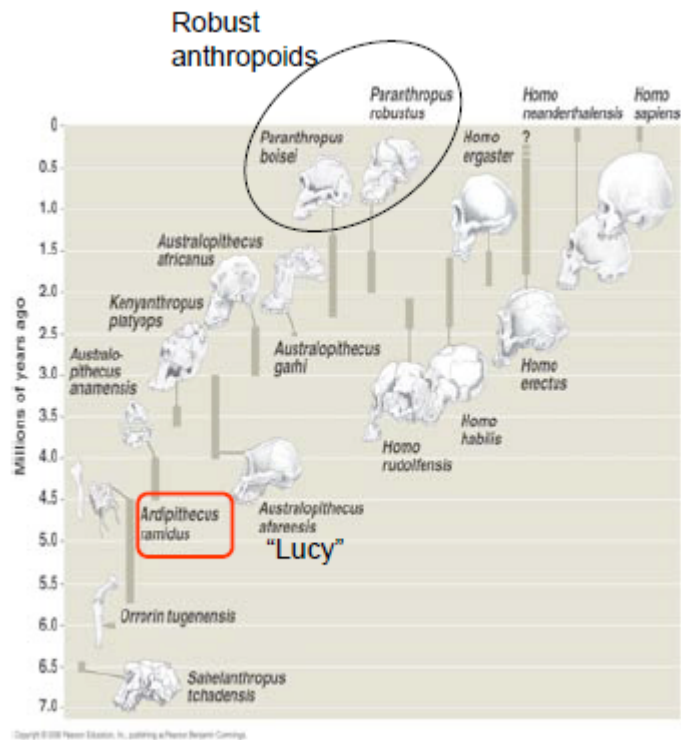


Figure 1: Plot of different hominins and their temporal location
Campbell, Fig 34.40, Copyright © 2008 Pearson Education, Inc., publishing as Pearson Benjamin Cummings

There was a large increase in diversity about 4-2mya in Africa.

Evolution of Homo and related hominins

Subfamily Homininae = monophyletic group consisting of humans, chimpanzees & gorillas and species now extinct within each of these lineages.

The fossil record provides evidence of the evolution of the Hominin lineage leading to *Homo sapiens*. There were two main schools of thought regarding the origin of *Homo sapiens*: Darwin thought humanity arose from Africa (due to presence of chimpanzees and gorillas), while other prominent scientists thought that humans arose out of Asia (due to presence of orangutans and early fossil Homo).

Key features shared by the lineage leading to humans include bipedalism (walking upright on two limbs) and smaller canines. There was a large increase in diversity about 4-2mya in Africa.

Evolution of *Homo*

Key *Homo* features include an increasing cranial case that allowed for a larger brain, decreased sexual dimorphism relative to their ancestors (and to Australopithecines), and more terrestrial behavior (walking on the ground rather than swinging through trees). Note that larger braincases came about later, although there is a debate in anthropological circles regarding whether our ancestors developed walking or larger brains first.

Homo erectus was first discovered in Indonesia (Java and Peking; you may have heard of the specimen known as “Java man”). However, the Leakeys (an archeologist family) discovered *Homo erectus* at a site called Olduvai Gorge in Africa. They also found *Homo habilis* (older) and *Paranthropus boisei* (even older) at that site. *Homo erectus* had a larger brain size than preceding species on this lineage. The most recent fossils of *Homo erectus* date back 27,000 years ago, though the identity of these is still debated – otherwise clear evidence for persistence to 200Kya.

Homo floresiensis was discovered in 2003 on the isle of Flores in southeast Indonesia. This was a small hominin, about a meter tall, with a lower braincase size than expected just from extrapolating from a brain: body ratio. Dating indicates the first discovered specimen is 12,000 years old, which is very recent, and overlaps *Homo sapiens*. (For context, consider that humans may have been practicing agriculture as early as 10,000 years ago and spread through Indonesia >45Kya). Other putative skeletal fossils date back to 75Kya and there are possible tools back to 51Kya – but again the latter are hard to interpret. One hypothesis is the first individuals found was a diseased microcephalic *Homo sapiens*. With additional fossils, this hypothesis is rejected if you examine other aspects of anatomy that have noticeably different characteristics than *Homo sapiens*.

Another possibility is that *Homo floresiensis* is indeed separate species (perhaps related to the much larger *Homo erectus*?) that has undergone **island dwarfism (aka insular dwarfism)**, a process where a community of large animals on an island experience a reduction in size. (The reverse can also occur, where small animals experience an increase in size.)

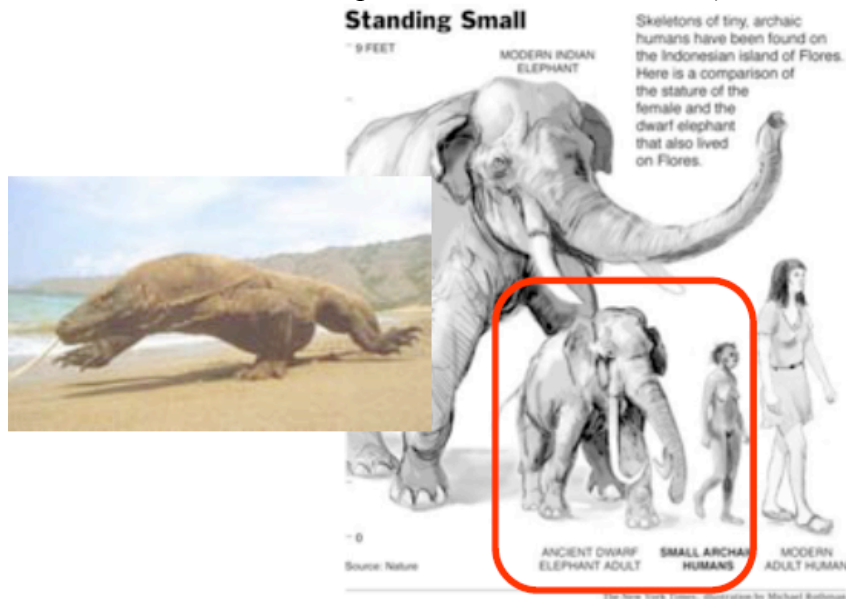


Figure 2: Giant lizards, tiny elephants (*Stegodons*), and *Homo floresiensis*
New York Times

Another example of insular dwarfism would be the elephants on the isle of Flores, as dwarf elephants (stegodons) were found in the fossil record on that isle. (Giant lizards similar to komodo dragons were also found on the island.). This exemplifies that species of *Homo* were subject to the same evolutionary pressures as other vertebrates living on islands.

Migration of *Homo sapiens*

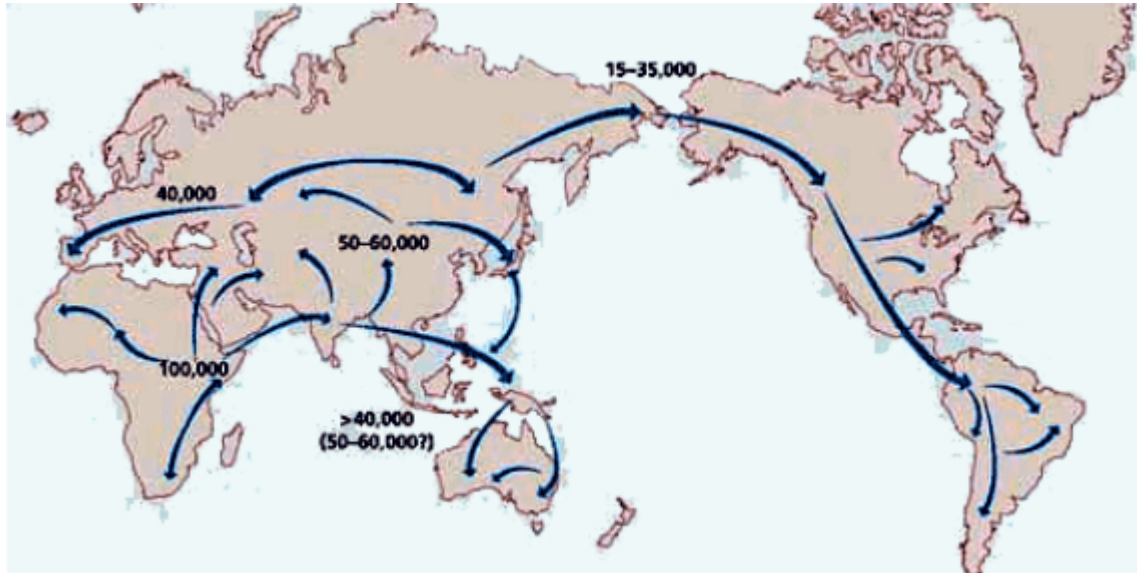


Figure 3: Map of *Homo sapiens* migration across the continents
Lecture 12, Craig Moritz

Following is a timeline based on fossil evidence, but it is supported by molecular data as well.

160 kya: *Homo sapiens* in Ethiopia

100 kya: migrates out of Africa into the Middle East and across South Asia

80 – 40 kya: migration from India to Australia, possibly interacting with *Homo erectus* in Indonesia

40 kya: migration into West Europe and across the range of *Homo neanderthalensis* (note: further north is covered by a glacial sheet)

35 – 11 kya: 1 or 2 migrations across the Bering land bridge

3.5 – 1 kya: Polynesian migrations to remote Pacific isles, e.g. New Zealand about 1Kya, Hawaii even more recent)

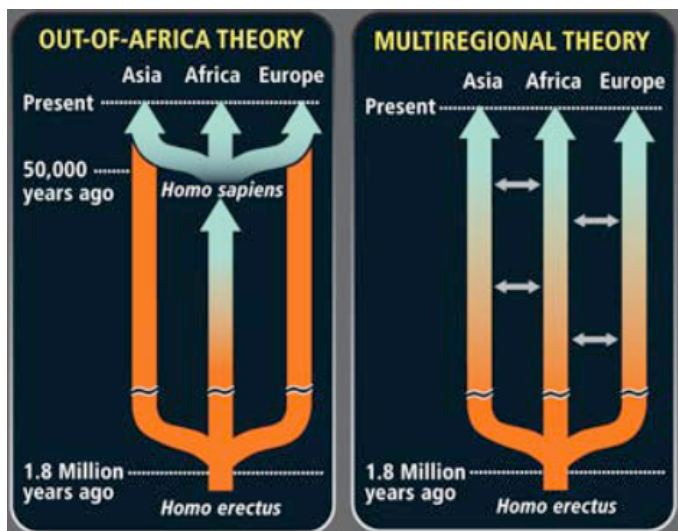


Figure 4: Multiregional and out-of-Africa theory
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There are two theories, the **multiregional** and the **out-of-Africa** theories. The second theory is the one more supported by molecular data.

The **multiregional** theory states that *Homo sapiens* arose independently in several locations from distinct populations of *Homo erectus*.

The **out-of-Africa** theory states that *Homo sapiens* arose in Africa and migrated out across the continent. Evidence for this includes high genetic diversity in African populations relative to non-African populations. (Think back to founder effects and population bottlenecks as to why this evidence supports the out-of-Africa theory.)

Interactions of *Homo sapiens* with *Homo erectus* and *Homo neanderthalensis*
Homo sapiens' eastward colonization took them through the range of *Homo erectus*, which still existed in the Indonesian archipelago, and *Homo floresiensis* as well. Their northern colonization brought them into the range of Neanderthals. Did *Homo sapiens* eradicate those other species? Or did they interbreed and thus absorb them into our population? Anatomical evidence from fossils can be interpreted either way

Recent analysis of genomes from Neanderthals compared to modern humans (from Paabo lab with Berkeley collaborators) demonstrate that about 2-3% of Eurasians and Papuans (= "Austronesians") are derived from Neanderthals. There is no such indication for Africans. Thus, there was some interbreeding as *H. sapiens* spread across the range of Neanderthals.

Even more surprising, genomic data from a fossil (one finger & one tooth) from a cave in Sth Siberia has revealed a distinct lineage – related to, but very different genetically from, Neanderthals (which themselves have very low diversity compared to modern humans). Without anatomical evidence, not clear whether these "Denisovans" should be described as a separate species of *Homo*. Key point is that genes from the Denisovan lineage turn up (at about 5%) in Papuans, but not Eurasians or Africans, suggesting interbreeding as *H. sapiens* initially moved across Asia towards New Guinea and Australia. No doubt more surprises to come from paleogenomics – wouldn't it be nice to have a genome from *H. floresiensis*!

Are humans still evolving?

As the architects of our own environments, are we still subject to natural selection? The answer is yes, just in different ways. Consider that the human population size has greatly increased, as has the ability for humans to migrate. Thus, while it has been relaxed, natural selection is likely now more important than genetic drift.

Consider also **lactose tolerance**. Lactase is an enzyme juvenile mammals have that breaks down lactose, allowing them to digest milk. Cats are the only mammals that maintain their lactase production into the adult stage of their life cycle – along with some humans, that is. Lactose intolerance is a retained ancestral condition; molecular comparison of the genes for lactase production show that the traits allowing human adults lactose tolerance arose independently in Northern Europe and in Africa at around the same time less than 5000 years ago. Lactose tolerance is an advantageous trait that has quickly been spreading throughout the human population.

Evolution and modern medicine

There are different factors to consider when considering diseases. Medicine has traditionally been focused on **proximate factors**: how did you get the disease, how does the disease work mechanistically and biologically, and how can we stop the disease? However, disease also has **ultimate factors**: what gave rise to this disease? In what populations did it evolve?

Evolutionary medicine has the following principles:

1. Understanding the evolutionary basis of diseases and the human phenotype can improve disease diagnosis, prevention, and treatment.

2. Variation in human phenotypes result from genetic variation and environmental influences on development.
3. Natural selection acts to maximize reproductive fitness, not health and longevity.

For more background on Evolutionary medicine, see the book chapter by Zimmer (2009) posted on the course website on the Evolution schedule under Lecture 12.

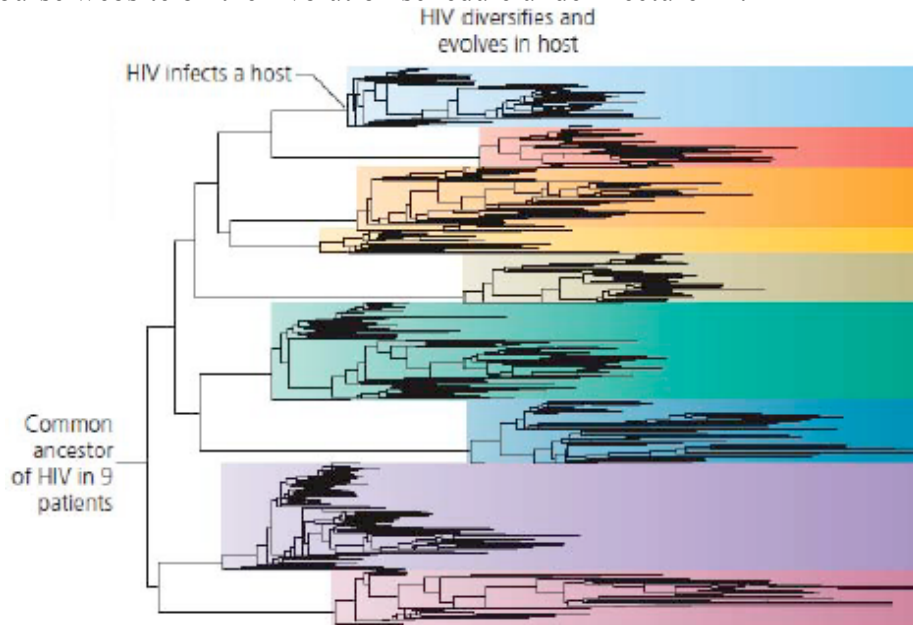


Figure 5: Rapid HIV evolution within hosts
© Zimmer 2009

We have already discussed the evolution of antibiotic-resistant pathogens. Another example involves HIV: once HIV infects a host, it undergoes rapid evolution within the host, creating many different strains within the host. There is not one virus to combat, but many, all with different properties.

Evolutionary mismatches: Some previously evolved human traits do not match our current environment due to rapid changes in human life-history (nutrition). For example, while sugar and fat were scarce resources in our evolutionary past, we now have constant access to a large supply of fat and sugar. If we eat all the fat and sugar we desire, we become obese or suffer from related conditions.

Consider: Like other species, *Homo sapiens* evolved to reach reproductive age and rear offspring, not to live beyond that age and reach a life-cycle stage that's never been selected for. Our bodies still suffer aging and eventual organ failure, but we also have conditions such as type II diabetes, cancers, and autoimmune deficiencies. These conditions may be the side effects of genes which allow us to reproduce earlier, but the negative results of which were never an issue before, simply because humans did not live that long – in effect, the short term reproductive gains always outshaded the long-term damages.

The **Thrifty Gene hypothesis** explains obesity in some populations. Certain groups have genes which ensure efficient metabolic processes, allowing infants to survive having scarce nutrition and nourishment. But when subjected to a diet rich in nutrition, fats, and sugars, they then make too much use of the available resources, becoming obese.

The **Hygiene Hypothesis** states that, with our constant battle to sanitize our living conditions, we have eliminated beneficial bacteria that we used to live in a symbiotic relationship with. As a result, we are now hypersensitive to any bacteria, and even to our own body, leading to autoimmune disorders..

Further Courses in Evolution:

IB 160 (Evolution)

IB 161 (Population Genetics)

IB 163 (Evolutionary Medicine)

IB 164 (Human genetics & genomics)

IB 166 (Evolutionary biogeography)

IB 183 (Evolution of the vertebrate skeleton)

IBc 185 (Human paleontology)

Anthro 1 (Biological Anthropology & human Evolution)