BIOLOGICAL ANTHROPOLOGY

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Biological anthropology, also known as physical anthropology, is a scientific discipline concerned with the biological and behavioral aspects of human beings, their related non-human primates and their extinct hominin ancestors. It is a subfield of anthropology that provides a biological perspective to the systematic study of human beings. This textbook explores evolutionary theory, including the core concepts of basic genetics and the modern synthesis of evolution. Students will examine, critically evaluate and explain scientific claims about the origins of humankind and modern human variation as well as biocultural evolution. Students will develop critical thinking and communication skills through the application of essential anthropological approaches, theories, and methods.

Thumbnail: The original complete skull (without upper teeth and mandible) of a 2,1 million years old Australopithecus africanus specimen so-called "Mrs. Ples" (catalogue number STS 5, Sterkfontein cave, hominid fossil number 5), discovered in South Africa . Collection of the Transvaal Museum, Northern Flagship Institute, Pretoria, South Africa. (CC BY-SA 4.0; José Braga; Didier Descouens).

CHAPTER OVERVIEW

I: Evolutionary Theory

Learning Objectives

At the end of this unit, students will be able to:

- answer the question, What is Biological Anthropology?
- explain the Scientific Method
- describe The History of Evolutionary Thought, including the roles of Charles Darwin & Darwinian Evolution
- relate Cell Biology & Genetics to molecular evolution
- apply Genetics & Evolution: Mendelian Genetics
- show how Genetics & Evolution: The Modern Synthesis works in population genetics
- discuss how population genetics applies to Human Variation & Race

In this unit students will learn about basic genetics, modern evolutionary theory, modern human variation, and the history of evolutionary thought.

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1.1: What is Biological Anthropology?

Anthropology is the scientific study of humankind. The main purpose of anthropology is for us to understand human biological and cultural diversity, and the origins of humans. So, the humans that anthropologists study can be modern or ancient, and can span across the globe. Anthropologists are unique in that they study the entirety of human existence over time and space.

***Figure* 1.1.1** - *Pride parade, Seattle, WA, June 26, 2011*

Basic tenets of anthropology:

1. **Holism**: Holism means that a part of something can only truly be understood if examined within relation to the whole of it. For anthropologists, this means that they try to understand humankind through the interrelationships of all aspects of human existence -- for example, human biology has to be examined within the context of human cultures and vice versa. In addition, all of this must be examined within the context of the environment and historical processes. In an effort to be holistic, anthropology is often an interdisciplinary field that crosses over into other fields such as history, geology, and ecology.
2. **Relativism**: Relativism means that judgments, truths, or moral values have no absolutes, and can only be understood relative to the situation or individuals involved. For anthropologists, this means that they accept that all cultures are of equal value and must be studied from a neutral point of view. A good anthropologist must disregard their own beliefs, morals, and judgments when examining another culture. They must, instead, examine each culture within the context of its own beliefs.
3. **Universalism**: Universalism means that whatever the theoretical principle is, it's equally applicable to all. For anthropologists, universalism means that we believe all humans are equal -- in intelligence, complexity, etc.This is in contrast to *ethnocentrism*, which is the belief that some peoples are more important or culturally/biologically better than other peoples.
4. **Culture**: All humans have culture. Culture is the set of learned behaviors and knowledge that belong to a certain set of people. This is different from genetically hardwired behaviors (such as reflexes) in that they aren't biologically inherited. The most important thing to remember is that culture is learned.

Subfields in Anthropology

There are four subfields in anthropology: cultural anthropology, biological (or physical) anthropology, archaeology, and linguistic anthropology.

- **Sociocultural Anthropology**

Sociocultural anthropologists examine social patterns and practices across cultures, with a special interest in how people live in particular places and how they organize, govern, and create meaning. A hallmark of sociocultural anthropology is its concern with similarities and differences, both within and among societies, and its attention to race, sexuality, class, gender, and nationality. Research in sociocultural anthropology is distinguished by its emphasis on participant observation, which involves placing oneself in the research context for extended periods of time to gain a first-hand sense of how local knowledge is put to work in grappling with practical problems of everyday life and with basic philosophical problems of knowledge, truth, power, and justice. Topics of concern to sociocultural anthropologists include such areas as health, work, ecology and environment, education, agriculture and development, and social change.

- **Biological (or Physical) Anthropology**

Biological anthropologists seek to understand how humans adapt to diverse environments, how biological and cultural processes work together to shape growth, development and behavior, and what causes disease and early death. In addition, they are interested in human biological origins, evolution and variation. They give primary attention to investigating questions having to do with evolutionary theory, our place in nature, adaptation and human biological variation. To understand these processes, biological anthropologists study other primates (primatology), the fossil record (paleoanthropology), prehistoric people (bioarchaeology), and the biology (e.g., health, cognition, hormones, growth and development) and genetics of living populations.

- **Archaeology**

Archaeologists study past peoples and cultures, from the deepest prehistory to the recent past, through the analysis of material remains, ranging from artifacts and evidence of past environments to architecture and landscapes. Material evidence, such as pottery, stone tools, animal bone, and remains of structures, is examined within the context of theoretical paradigms, to address such topics as the formation of social groupings, ideologies, subsistence patterns, and interaction with the environment. Like other areas of anthropology, archaeology is a comparative discipline; it assumes basic human continuities over time and place, but also recognizes that every society is the product of its own particular history and that within every society there are commonalities as well as variation.

- **Linguistic Anthropology**

Linguistic anthropology is the comparative study of ways in which language reflects and influences social life. It explores the many ways in which language practices define patterns of communication, formulate categories of social identity and group membership, organize large-scale cultural beliefs and ideologies, and, in conjunction with other forms of meaning-making, equip people with common cultural representations of their natural and social worlds. Linguistic anthropology shares with anthropology in general a concern to understand power, inequality, and social change, particularly as these are constructed and represented through language and discourse.

(From: American Anthropological Association. 2015. What is Anthropology? <http://www.aaanet.org/about/WhatisAnthropology.cfm>. Accessed 2015 May 7.)

While the sheer scope of anthropological study requires people to choose a subfield and specialization within that subfield many anthropologists integrate multiple subfields in their work. It is common to find biological anthropologists working with cultural anthropologists to examine things such as disease patterns and archaeologists to look at migration patterns in the past.

What is Biological Anthropology?

***Figure 1.1.2**: Heather Hecht Edgar (University of New Mexico) conducting research at the Czech National Museum, 2005*

Biological anthropology is the study of the biology of humans and their nearest biological relatives. "Biological relatives" include both humankind's ancestors and our nearest living relatives, the non-human primates. Biological anthropologists fall under 3 major categories:

1. Human biology (human biological diversity, genetics, adaptations to environmental stressors, etc.)
2. Primatology (non-human primate biology, evolution, behavior, ecology, etc.)
3. Paleoanthropology (human origins and human evolution)

These are the topics we'll be studying in this course. Each unit follows each of the 3 major categories found in biological anthropology.

- Unit 1: In this unit, you'll learn the basic toolkit you'll need (evolutionary theory) in order to understand the rest of the course. This unit also covers human biology.

- Unit 2: This unit covers primatology.
- Unit 3: This unit covers paleoanthropology.

1.2: Scientific Method

Science is a way to gain knowledge about natural phenomena using empirical observation and testing (Jurmain, et al 2013). While there are different protocols used in science, it is performed using a set of rules called **The Scientific Method** that guide scientific practice (Fancher 2000). The method stresses the need to develop a testable hypothesis, the use of objectivity and rationality, and the circularity of scientific research. This does not mean that science is infallible, but in using the scientific method, particularly with the necessity to have testable hypotheses and tests that are replicable by other researchers, rigorous conclusions are reached.

Why do students of biological anthropology need to understand the scientifc method? Because anthropology is a science.

Steps of the Scientific Method

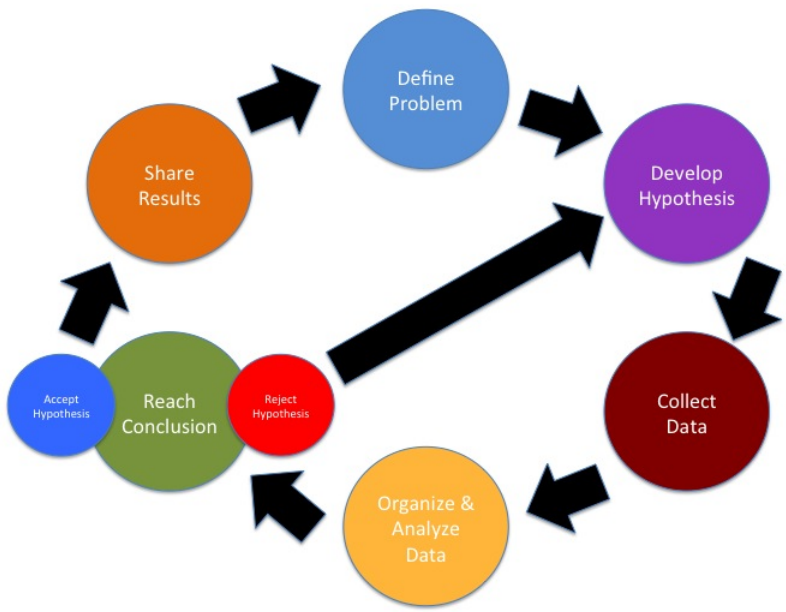

Figure 1.2.1 *- Diagram of the scientific method*

1. Define the problem

    This is based on observation -- either something you've observed from nature or from something that's already been written. How many times have you seen something or read about something and thought up a question about it? If you have, then you've done the first step of the Scientific Method!

2. Develop Hypothesis

    Propose an explanation for the observed phenomenon. For a hypothesis to be a GOOD hypothesis, it must be testable. In other words, you must be ABLE to test it to see if it's supported or not supported. A hypothesis is still good, even if it's unsupported, as long as it's testable. There are lots of questions out there that are untestable, such as, "Somewhere on the planet, a pink elephant is dancing the can-can in a tutu." Because it's impossible to explore every inch of the world looking for our dancing elephant, this would not be feasibly testable. Along the same lines, a testable hypothesis would be, "Student group A, who have read the material on The Scientific Method, will have a higher average score on their quiz than will Student group B, who have not read the material on The Scientific Method."

3. Collect Data

    The experiment should be specifically designed to test the hypothesis. The experiment will provide data as to whether the hypothesis is supported or not. Experiments must be replicable by other researchers. For our example above with ever-so-fortunate quiz-takers, you'd have Group A read the material (Group B would not) and both groups would take the quiz. This experimental design is replicable by other researchers because they too could find two groups of students, and follow the same protocol (one group reads the material, one not, and both take the quiz).

4. Organize/analyze data:

 Once the experiment is completed, you must organize the data and analyze the results. For our example, you would grade the quizzes and calculate the average score per group.

5. Conclusion

 You develop a statement that sums up what the data (collected during the experimental phase) says about the hypothesis. For our example, our concluding statement would be something like, "Group A, who read material on The Scientific Method, performed better on a Scientific Method quiz than did Group B, who did not read the material." If your hypothesis is supported, then you would move on to the next step in the process. If your hypothesis was not supported you would rework your hypothesis and start the process over.

6. Share the knowledge

 It is important to share the results of your work even (and maybe even *especially*) if your hypothesis was not supported. This hasn't been a step in the "old school version" of The Scientific Method, but remember -- information is only good if it's communicated to others!

Things to keep in mind:

- Science does not "prove" anything. Hypotheses are falsified/supported or not falsified/supported. For a hypothesis to be accepted as a theory, which is a generally accepted explanation of specific phenomena, it undergoes rigorous testing (Larsen 2008: 16). It can take decades for a hypothesis to become a theory.
- While we discuss various topics in biological anthropology that each piece of information was once a hypothesis that was tested and supported by the data. Contradictory supported-hypotheses are possible; some refer to this as **equifinality**. This just means that the data collected supports two (or more) hypotheses -- in most cases, there is not sufficient data available to support one more than the other (especially when we get to the information within human evolution). Hopefully, in these cases, one day we'll have enough evidence to overwhelmingly support one particular hypothesis, but at the present that's not possible. So, for the moment we have to open our minds to accept two potential conclusions.

The Scientific Method in Action!!! Watch the following clip and identify the steps of The Scientific Method. Was their hypothesis testable? Was their experiment replicable? What was the conclusion of their "scientific endeavor"? Clip: The Scientific Method in Action

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1.3: History of Evolutionary Thought

Contrary to popular opinion, evolutionary thought does not start with Charles Darwin. The history of evolutionary thought is a fascinating story spanning hundreds of years of both speculation and scientific discovery. Using the links below, explore the story from early studies of earth sciences, through 20th-century discoveries that enrich our understanding of life on earth. As you read each person's contribution, pay particular attention as to what exactly is the key contribution for evolutionary theory. Sometimes this will be clear, while other times it might be a bit more murky.

When navigating US Berkeley's *Understanding Evolution: The History of Evolutionary Thought* web-site, make sure you click on "next page" when you see it. All of the links below go to different pages on the *Understanding Evolution* web site. They are provided here so that you do not have to continually go the first page should you decide to read these pages in different sittings.

- **Pre-1800s**
  - Comparative Anatomy: Vesalius
  - Observation: Harvey & Palin
  - Fossils & Paleontology: Steno
  - Nested Hierarchies: Linneaus
  - Ancient Life: Leclerc & Buffon
  - Human Ecology: Malthus
- **1800-1900**
  - Extinction: Cuvier
  - Evolution Happens: Lamarck
  - Developmental Similarities: von Baer
  - Biostratigraphy: Smith
  - Uniformitarianism: Lyell
  - Discrete Genes: Mendel
  - Early Evolution and Development: Haeckel
  - Biogeography: Wallace & Wegener
  - Fossil Hominids: Huxley & Dubois
  - Chromosomes and Mutations: Morgan
- **1900-Present**
  - Random Mutation: Fisher, Haldane & Wright
  - The Modern Synthesis: Dobzhansky
  - Speciation: Mayr
  - DNA: Crick & Watson
  - Radiometric Dating: Clair Patterson
  - Endosymbiosis: Lynn Margulis
  - Evolution and Development for the 21st Century: Gould
  - Genetic Similarities: Wilson, Sarich, Sibley & Ahlquist

You may notice that Darwin is absent from the list above although you may have read about him if you followed the links on the *Understanding Evolution* website. That is because there is a special page devoted to Darwin. Even if you read the *Understanding Evolution* page you need to read the page included on this textmap.

1.4: Darwinian Evolution

Who was Charles Darwin?

Ernst Mayr claims, and many would agree, that Charles Darwin has done more to influence the philosophy of science, evolutionary biology, and the modern zeitgeist than any other individual (Mayr 2000: 78). Darwin developed a comprehensive biological theory of evolution that provided a unity to the natural world never before seen. He demonstrated the importance of historicity in science as well as a methodology that involved observation, comparison and classification, not just experimentation. Darwin's ideas, which rocked the foundation of Western society, still create heated debate in the modern world (Mayr 2000). So, just who was Charles Darwin?

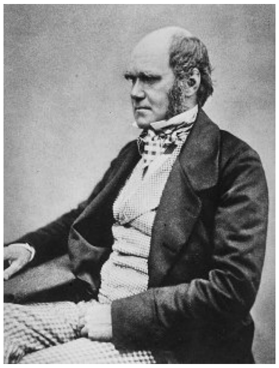

***Figure* 1.4.1** - *Charles Darwin in 1854*

> For a quick introduction to Darwin, watch the PBS video "Who was Charles Darwin?"

Darwin: The Early Years

Darwin was born on February 12, 1809 in Shrewsbury, England. His father, Robert, and grandfather, Erasmus, were both physicians. His mother, Susannah, was a part of the Wedgwood family, famous even today for their fine china. Erasmus Darwin is remembered for his work *Zoonomia*, which attempts to explain the natural world using evolutionary principles (Mayr 2000). It is clear that Darwin was introduced to current intellectual thought about evolution when he was young (Darwin 1887).

Darwin grew up with a love of the natural world. Darwin himself tells us that early on he developed a love of travel and collecting things, including minerals and insects:

> *With respect to science, I continued collecting minerals with much zeal, but quite unscientifically—all that I cared about was a new-named mineral, and I hardly attempted to classify them. I must have observed insects with some little care, for when ten years old (1819) I went for three weeks to Plas Edwards on the sea-coast in Wales, I was very much interested and surprised at seeing a large black and scarlet Hemipterous insect, many moths (Zygæna), and a Cicindela which are not found in Shropshire. I almost made up my mind to begin collecting all the insects which I could find dead, for on consulting my sister I concluded that it was not right to kill insects for the sake of making a collection. From reading White's 'Selborne,' I took much pleasure in watching the habits of birds, and even made notes on the subject. In my simplicity I remember wondering why every gentleman did not become an ornithologist. -Darwin 1887: 34-35*

Darwin carried this love of the natural world to the University of Edinburgh, where he was introduced to the work of Cuvier, Lamarck, and Saint-Hilaire (Young 2007), and subsequently, the University of Cambridge. At Edinburgh, Darwin studied medicine, but when it became apparent that the young Darwin had no interest in medicine, his father sent him to study theology at Cambridge. It was at Cambridge that Darwin's love of natural history flourished. He studied and worked with noted botanist J. S. Henslow, who would be instrumental in getting Darwin on the H.M.S. Beagle, scientific generalist, William Whewell, and geologist, Adam Sedgwick, all of whom were influential in his intellectual development, although Henslow would be the most critical individual in Darwin's post-college life (Bowler 1992, Mayr 1991, Young 2007). While at Cambridge, Darwin became an avid collector of beetles. This activity helped him become familiar with comparative anatomy, a methodology that would be critical to the development of his evolutionary theory.

> *The pretty Panagaus crux-major was a treasure in those days, and here at Down I saw a beetle running across a walk, and on picking it up instantly perceived that it differed slightly from P. crux-major, and it turned out to be P. quadripunctatus, which is only a variety or closely allied species, differing from it very slightly in outline (Darwin 1887:51),*

After graduating from Cambridge, Henslow helped Darwin secure a position aboard the H.M.S. Beagle as the ship's naturalist. He almost did not make the trip as his father was against it, but his uncle, Josiah Wedgwood, convinced Darwin's father to let him go on the voyage (Eldredge 2005). The Beagle, under the captaincy of Robert Fitzroy, left England on December 27, 1831 with the goal of charting the waters of South America (Bowler 1992, Futuyma 1986). While on the Beagle, Darwin, who was still an orthodox member of the Church of England (Futuyma 1986), made numerous observations that would eventually lead him to develop his theory of evolution by natural selection.

The Beagle Voyage

During the five years Darwin was on board the Beagle, he read such scientific works as Charles Lyell's *Principles of Geology* and made observations that eventually led him to question his belief in the fixity of species, a commonly held notion that species were unchanging and perfect in their environment. He collected fossils, rocks, plants and animals, many of which were shipped back to England where eventually specialists such as the ornithologist John Gould examined the specimens. Darwin's discovery of a new species of the rhea living in the same area as the already known rhea raised questions about perfect adaptation...if it were true, why would there be two species of rhea in the same area [1]? However, it was the Beagle's stop in the Galápagos Islands that would be most important for the later development of his theory.

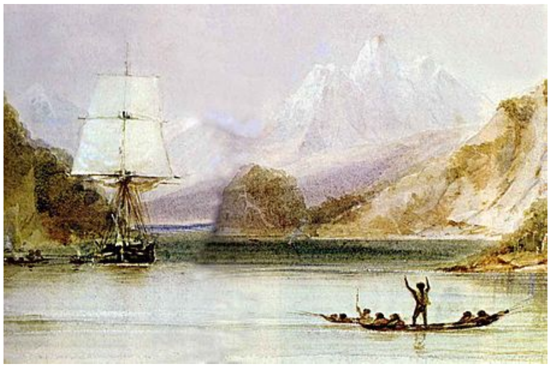

***Figure* 1.4.2** - *HMS Beagle by Conrad Martens.*

In the Galapagos, Darwin studied birds, iguanas and tortoises. The natives of the Galápagos showed Darwin how to determine which island the tortoises came from based on the shape of their shells. After learning this, he returned to the birds he had collected while in the Galápagos and sorted them by island. This gave Darwin, "...an unrivalled [*sic*] opportunity to study the effects of geographical isolation in the production of new species" (Bowler 1992: 300). It would be the Galápagos birds, specifically the mockingbirds, that would lead Darwin to his ideas about natural selection (learn more about the mockingbirds).

> To read some of Darwin's journal entries for the voyage, check out The Beagle Voyage or for a complete collection, see Journal of Researches

> You can follow the Beagle voyage, read quotes and view sketches from Darwin's diary by visiting the Natural History Museum's Big Idea Big Exhibition.

After the Beagle

Upon his return to England in October 1836, Darwin plunged himself into the scientific community of London. He had worked hard while on the Beagle so that he would not have to become a clergyman.

> *As far as I can judge of myself, I worked to the utmost during the voyage from the mere pleasure of investigation, and from my strong desire to add a few facts to the great mass*

> *of facts in Natural Science. But I was also ambitious to take a fair place among scientific men--whether more ambitious or less so than most of my fellow-workers, I can form no opinion (Charles Darwin quoted in Eldredge 2005: 27).*

Henslow and Lyell had made Darwin well known in scientific circles while he was still at sea, so he readily became active in the Geological Society (Bowler 1992, Eldredge 2005) and the Athenaeum Club, a gentlemen's club that served as a meeting place for those of an intellectual bent (Eldredge 2005).

One of the first things Darwin did on his return was to organize and ship his collections to various specialists. Ornithologist John Gould quickly examined Darwin's collection of birds, informing him that the mockingbirds in the collection were in fact different species of mockingbirds, some from the various Galápagos Islands and some from the South American mainland. Darwin theorized that this could only be explained if the island birds' antecedents had found their way from the mainland to the islands. Once there, the descendents were gradually modified until they became new species (Young 2007: 108). Here we find Darwin's coherent thoughts on the role geographic isolation has in speciation, or the creation of new species. By March 1837, Darwin had rejected the idea of the fixity of species and creation by design and accepted the idea of evolution and the role of geographic isolation in speciation (Futuyma 1986, Mayr 1991).

In July 1837, Darwin opened his first notebook, 'Transmutation of Species,' which during this time in history was code for evolution. In this notebook, Darwin explored ideas about reproduction and variation and the nature of species. By the time he concluded this notebook, Darwin has laid out his ideas on common descent and branching evolution. What he still didn't know at this point was how it all occured (Young 2007).

A year later, Darwin began his studies of artificial selection. His second notebook outlines his thoughts on variation and inheritance and their relation to adaptation (Young 2007). Darwin's studies of artificial selection helped him understand how a natural mechanism might work (Bowler 1992). Breeders at the time talked about something akin to natural selection but only in the context of how it kept species and varieties "true to type" (Young 2007: 112). When Darwin read Thomas Malthus's work, An Essay on the Principle of Population, in 1838, the concepts Malthus outlined on exponential population growth and competition among members of a population for a limited food supply provided the crucial piece that was missing. Darwin realized that in light of competition among members of a population, variations of traits that allowed one member to have an advantage over other member would be preserved. He further concluded that disadvantageous variations would die out (Young 2007). Darwin now understood how it all occurred for all of nature, including humans.

> *As soon as I had become, in the year 1837 or 1838, convinced that species are mutable productions, I could not avoid the belief that man must come from under the same law (Darwin quoted in Eldredge 2005: 29.).*

Darwin married his cousin, Emma Wedgwood, in 1839. By 1842, the Darwins moved from London to Downe in Kent in order for their children to grow up in the country and also for Darwin's health. In his later years, Darwin was plagued with ill health. While we do not know exactly from what he suffered, the symptoms suggest a malfunctioning of the autonomous nervous system (Mayr 1991).

Figure **1.4.3** - *Emma Wedgwood Darwin.*

In 1842, Darwin outlined his ideas on evolution by natural selection, expanding further in an 1844 essay that was to published only upon the event of his premature death. Bowler (1992) suggests Darwin did not publish at this time for two reasons: 1) the social climate--there was quite a bit of debate over Lamarck's theory of evolution and Robert Chambers' *Vestiges* that discussed evolution as part of a divine plan, and 2) he could not explain why the fossil record showed "...that many families had been subject to a constant trend towards increasing levels of specialization" (Bowler 1992: 304). The answer to this question would come a decade later when Darwin figured out that specialization provided an advantage even if the environment was stable because it cut down on competition for resources (Bowler 1992). During his time at Downe, Darwin used the hypothetico-deductive method (more commonly known as the scientific method) to build his case for evolution by natural selection, particularly in his work with pigeons (Young 2007).

Darwin began to write his "Big Species" book in 1856. He first published his ideas in 1858 after receiving a manuscript from Alfred Russel Wallace that outlined his ideas on natural selection, which coincided with Darwin's. At the urging of close friends in the scientific community, Darwin quickly put together a paper based on his 1844 essay that was presented by Charles Lyell and Joseph Hooker at the Linnean Society on July 1, 1858 along with Wallace's manuscript. Darwin then set to work on putting together an abstract of his Big Species book, which was published in 1859. This abstract, *On the Origin of Species by Natural Selection*, sold out in one day (Futuyma 1986, Mayr 1991, Young 2007). It was "the book that shook the world" (Mayr 1991: 7).

After the publication of *Origin*, Darwin's work focused on expanding on ideas that were touched on in the abstract, but not completely described. His other contributions to biology include *The Variation of Animals and Plants under Domestication* (1868), *The Descent of Man and Selection in Relation to Sex* (1871), *The Expression of the Emotions in Man and Animals* (1872), *Insectivorous Plants* (1875), *The Effects of Cross- and Fertilization in the Vegetable Kingdom* (1876), *The Different Forms of Flowers on Plants of the Same Species* (1877), *The Power of Movement in Plants* (1880 with Sir Francis Darwin), and *The Formation of Vegetable Mold, through the Action of Worms, with Observations on Their Habits* (1881).

Darwin died in 1882, but his work continued to be reviewed and oftentimes vilified by philosophers, theologians, scientists. etc. Darwin had a number of friends that supported his work both before and after his death, and while most scientists of the time came to support Darwin's proposal about common descent, few adhered to his concept of natural selection (Mayr 1991). It would not be until the 1920s when a fundamental change occurred in the thinking about organisms that the true genius of Darwin's work would be recognized on a broader scale (Futuyma 1986).

Darwin's contribution is summed up nicely by Futuyma (1986:6):

> *Darwin was the first to marshall on so grand a scale the evidence of the first thesis [i.e., descent with modification from a common ancestor], the historical reality of evolution by drawing on all relevant sources of information: the fossil record, the geographic distribution of species, comparative anatomy and embryology, and the modification of domesticated organisms.*

Mayr (1992) states that Darwin was unique among scientists of his day because he was not only a great naturalist and biologist, but was a great theoretician and experimenter. It was these differences that allowed him to make links across fields and develop his comprehensive, complex theor(ies) of evolution.

The Theory of Descent with Modification through Natural Selection

All information in this subsection is drawn from Mayr 1991.

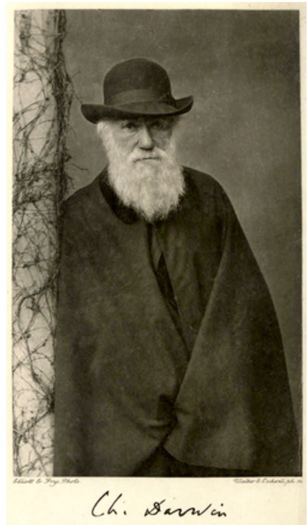

***Figure* 1.4.4** *- Charles Darwin photographic portrait, 1881*

Darwin's theory is actually a series of five theories:

1. Evolution as such: species are not immutable; they change slowly and steadily over time. This idea challenged the commonly held belief that there was a perfect design to life on earth.
2. Common descent: groups of organisms come from a common ancestor and all organisms ultimately originate from a single origin of life on earth. This idea provided a unity to biological life that had never been seen before.
3. Multiplication of species: geographic isolation lead to the evolution of new species. This idea explained the natural biological diversity on earth.
4. Gradualism: change occurs over long periods of time. This idea was in opposition to the contention that new species arose suddenly (saltation).
5. Natural selection: those individuals with variations (traits) best suited to enable an individual to reproduce within an environment are more likely to pass on their traits to next generation. Each generation would produce more variation, when again, the traits best suited to enable survival would be passed on. The classic example of natural selection in action is the peppered moth. Learn more about this moth by watching a short video on YouTube or read this short article from the State University of New York.

But there were some things that Darwin didn't know, namely, how traits were inherited or what caused variation within a population. Darwin also could not account for how similar species got on different continents, e.g., the ostrich in Africa and the rhea in South America. It would take decades for geologists to develop the theory of plate tectonics. Geologists in Darwin's day did not estimate the earth over 100 million years old, not enough time for evolution to work, but none of these things take away from the brilliancy or resiliency of Darwin's work. Over 100 years of testing has refined Darwin's theory while at the same time demonstrating over and over that his basic ideas, particularly natural selection, hold true. For more on what Darwin didn't know when he published his theory, check out this article from the Smithsonian Magazine.

What was it about Darwin's theory that "shook the world"? Some of his ideas challenged religious dogma and others challenged secular philosophies. Religious dogma that was directly challenged was the belief in the constancy of the world. The predominant belief in Europe and the United States was that while there had been a few catastrophes, e.g., Noah's flood, the world remained unchanged from when it was created approximately 6000 years ago by a devine Creator. All organisms were created to perfectly adapted to their environment, therefore, they did not change. Man (and it was the common vernacular of the time), with his unique soul, was separate from the rest of nature. In the arena of secular philosophy, Darwin's ideas challenged essentialism, or the fixed properties of an entity, the "...causal processes of nature as they had been elaborated by the physicists" (Mayr 1991: 39), e.g., Newton, and teleology, or a pre-determined end. While science has tested and retested Darwin's ideas and subsequently developed a synthetic theory of evolution (the modern synthesis), the debate continues on in many religious circles. To read more about the modern debate between religion and evolution visit the Talk Origins "God and Evolution" page.

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1.5: Cell Biology and Basic Genetics

When Darwin developed his theory, there are two main things that he did not know: (1)where the variation comes from, and (2) how the traits are passed from one generation to the next. In the decades since *On the Origin of Species* was published, subsequent generations of biologists, natural scientists, geneticists, paleoanthropologists, etc., have conducted research that has refined our knowledge about evolution. We now can address the things that Darwin did not know. Cell biology and genetics explain where variation comes from and how those traits are inherited.

Cell biology

All living organisms are made of ***cells***. Some organisms are single-celled and spend their life made of just one cell and some organisms, like humans, are multi-cellular (have many cells). Here are some basic points that you always have to remember about cells:

- cells are the structural and functional units of all living things
- all cells come from pre-existing cells
- cells contain hereditary information (which is passed from "parent" cells to "daughter" cells during cell division).

Cell function

Cells are often called "the building blocks of life". Not only are all living things made of cells (the 'building block' part), they also are living functional units themselves. This is because cells do the following:

- obtain nutrients and other molecules through the cellular membrane (or cell wall) and convert that to biologically useful energy and useful molecules for building new cells (such as proteins and nucleic acids)
- make more cells (reproduction)

Types of cells

There are two types of cells: prokaryotic and eukaryotic. Prokaryotes include bacteria and blue-green algae. These are single-celled organisms in which the genetic material is not distinctly separated from the other components of the cell. Eukaryotes include everyone else. These can be single-celled, but are more often multi-celled organisms in which the genetic material is separated from all of the other cellular components (by something called the **nucleus**). Because our focus is on humans, the rest of our discussion will center on eukaryotes and eukaryotic cells.

Cell structure

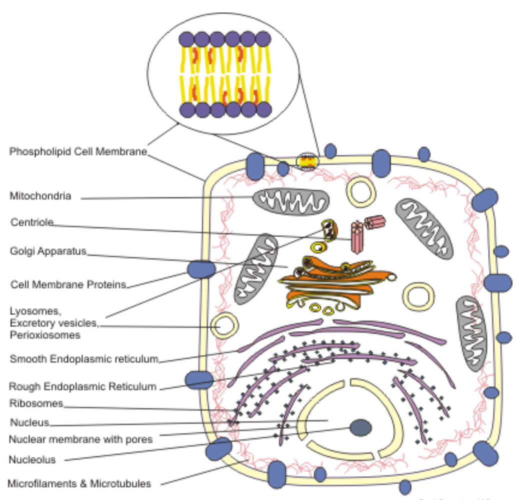

Figure **1.5.1** - *A typical animal cell and its parts*

Each animal cell consists of a selectively permeable membrane (plants have cell walls) which contains the cytoplasm.

Organelles are like "little organs" within the cytoplasm, each performing a different vital cellular function. These are some of the more important (to us) organelles.

- Mitochondria: These are the "powerhouses" of the cell, responsible for production of the energy-rich molecule, ATP (adenine triphosphate), which powers the activities of the cell. Each cell has hundreds to thousands of mitochondria. Mitochondria have their own DNA, known as mitochondrial DNA (mtDNA), which is different from nuclear DNA (see below). Mitochondrial DNA has become an important tool in evolutionary research.
- Endoplasmic reticulum: This is a transport network for molecules that have specific destinations or require certain modifications. It comes in two types: smooth and rough. Rough endoplasmic reticulum has ribosomes (see below) on the surface.
- Golgi apparatus: Processes and packages large molecules such as proteins and lipids (fats) that are produced by the cell.
- Lysosomes: Breaks down non-usable organelles, food, viruses, and bacteria using enzymes.
- Ribosomes: Protein synthesis
- Nucleus: This is where you'll find the hereditary material, DNA (deoxyribonucleic acid) and RNA (ribonucleic acid).

Exercise 1.5.1

Explore the cell!!

In this interactive exercise, you can identify the parts of a typical animal cell and review the functions of the various organelles.

Typical animal cell

DNA

DNA (deoxyribonucleic acid) is the genetic blueprint of the cell. The structure of DNA is what's known as a "double helix", which looks much like a twisted ladder. The basic unit of DNA is a molecule called a nucleotide. Nucleotides are made of a sugar (deoxyribonucleic acid), a phosphate group, and a nitrogenous base. There are 4 different types of nucleotides, depending on what type of nitrogenous base they have.

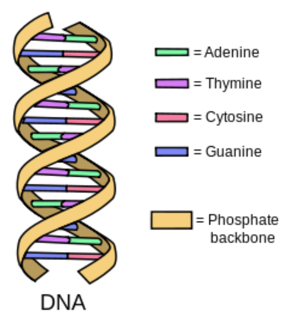

***Figure* 1.5.2** - *DNA structure*

- adenine (A)
- thymine (T)
- cytosine (C)
- guanine (G)

These are separated into 2 groups:

- purines: adenine and guanine
- pyrimidines: cytosine and thymine

On the DNA "rungs", the bases must go in pairs: adenine (A) always bonds with thymine (T) and cytosine (C) with guanine (G). So, for base-pairs remember it's always A+T and C+G! (That rule is sometimes called "The base-pair rule".) If you want to explore further, check out what the Human Genome Project has learned about the human DNA sequence

RNA structure

RNA (ribonucleic acid) has a very similar structure to DNA, except that it's single-stranded, has a different sugar (ribonucleic acid, rather than deoxyribonucleic acid), and does not contain thymine (T). Instead, it contains uracil (U), which like thymine, bonds with adenine (A). So, in this case, the base-pair rule is A+U and C+G.

DNA function

For our purposes, we will concern ourselves with two of DNA's functions: replication and protein synthesis.

DNA replication

In this case, the goal is to replicate a DNA double helix to produce more DNA. DNA replication occurs in the nucleus of the cell.

The basic steps of DNA replication are:

1) The DNA is "unzipped" into two single strands.

2) Each unzipped strand acts as a template for reproduction of the complimentary strand.

3) The product is two copies of the original DNA, each containing one strand from the original DNA and one strand that has been added on.

Here's a slightly more thorough illustration of the process: DNA replication - simple.

And for those who are really curious about the details of the process: DNA replication - complex.

And for those who are looking for a little fun with their DNA replication: DNA - the double helix game

Important note: The important thing to remember about DNA replication is that when the complimentary strand is created, sometimes accidents or mistakes happen. For example, a G gets matched up with a T instead of the proper A. This is where some of the variation in hereditary information comes from.

Protein synthesis

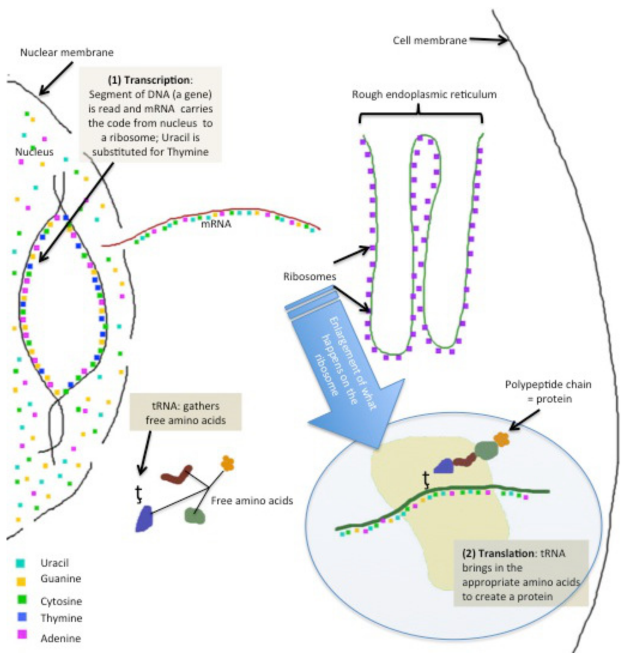

***Figure* 1.5.3** - *Protein synthesis*

Proteins are the most common large molecules in cells. Bones, muscles, and red blood cells (among lots of other body parts) are made mostly of proteins. Therefore, the production of proteins is obviously a very important process in the body.

Proteins are made of smaller units called amino acids. There are 20 different amino acids, 9 of which are "essential amino acids", which means that they must be consumed through the diet, rather than being synthesized by the body. The sequence of amino acids in a protein determines its structure and function.

The base pair sequence of the DNA molecule is known as **the genetic code**. The genetic code consists of 3-base sequences called **codons**.(Remember our friends A, T, G, and C -- the nitrogenous bases? That's what we're talking about here.) Each codon either codes for an amino acid, or signals that the protein chain is starting (an initiation codon) or stopping (a termination codon). The table on the right shows which codons code for which amino acids.

Each DNA molecule contains the information to make up many different proteins. A portion of a DNA molecule responsible for making up a single protein (or sometimes just part of a protein, called a polypeptide) is a **gene**. Therefore, each DNA molecule consists of many genes, that code for many proteins.

Protein synthesis has two basic steps: (1) transcription and (2) translation.

Definitions

Transcription

1) The gene (DNA) is copied onto RNA. The RNA copy of the gene is called the messenger RNA (or mRNA).

2) The mRNA leaves the nucleus and goes to the rough endoplasmic reticulum. (Remember this organelle from the cell structure section above?)

Translation

1) The mRNA goes into the ribosomes, where tRNA (translation RNA) reads the mRNA.

2) As the tRNA reads the mRNA, it attaches complementary amino acids to the newly synthesized amino acid chain (AKA the growing protein chain).

Note

Important note: The important thing to remember about protein synthesis is that when a protein is synthesized, sometimes accidents or mistakes happen. This is where some of the variation in protein synthesis comes from. Additionally, remember the possible mistakes in DNA replication? If the original DNA strand is changed so that a gene is altered, that can affect protein synthesis as well.

This video has fantastic digital animations illustrating DNA replication and protein synthesis.

Cell replication

To make more cells, we not only have to have replicated DNA, we have to replicate the rest of the cell as well in order to physically divide that replicated DNA. For body cells (AKA somatic cells), this process is called **mitosis**. For sex cells (AKA sperm and eggs), this process is called **meiosis**. But first, a little bit about DNA and chromosomes.

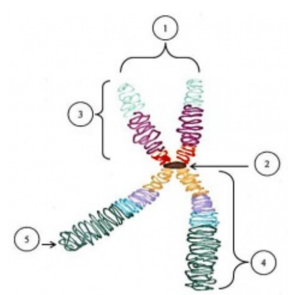

***Figure* 1.5.4** - *Chromosome*

Chromosomes

Most of the time, DNA in cells is in loosely arranged, dispersed strands. When DNA is like this, it's called **chromatin**. However, during cell replication DNA condenses into structures called **chromosomes**.

Each chromosome is made of (the numbers reference the illustration to the right): 1) two "sister" chromatids, 2) a centromere, which is a highly condensed area on the chromosome, 3) the "short arm" of the chromatid, 4) the "long arm" of the chromatid, and the 5) telomere, which is the end of a chromosome and is involved in both replication and chromosomal stability. In this diagram, the different colors represent genes on the chromosome.

Each somatic cell (sex cells are different) has the same number of chromosomes. This number is consistent within species, but often differs between species. The number of chromosomes in each body cell is called the **diploid number**. Sex cells have half as many chromosomes as do somatic cells. This number is called the **haploid number**.

Most species have two copies of each chromosome in each somatic cell. The member-chromosomes of each pair are called **homologous chromosomes**.

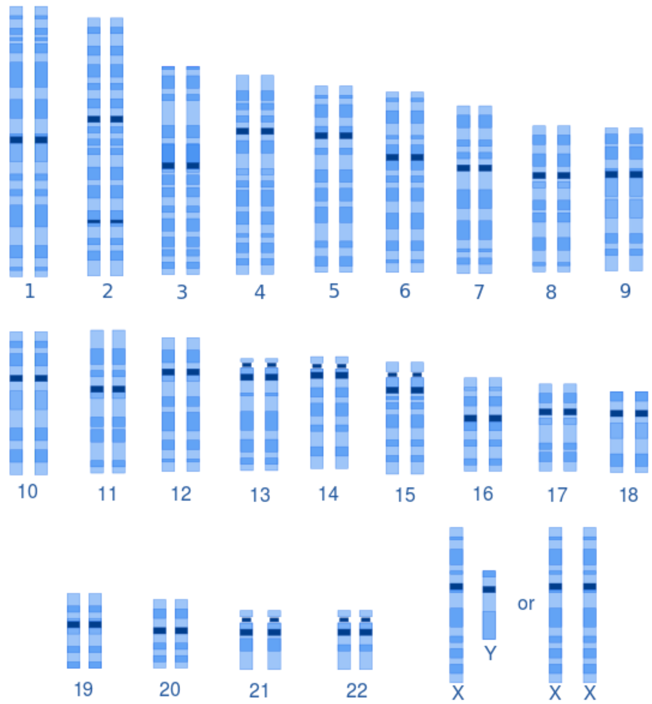

***Figure* 1.5.5** - *A typical human (male) karyotype*

On the left is a **karyotype**, which is an image of the full diploid complement of chromosomes from an individual. Above each number is each pair of homologous chromosomes. This is from a human, who typically have 23 pairs of chromosomes in each somatic cell, for a diploid total of 46 chromosomes. For humans, sex cells normally have 23 chromosomes.

Genes are found on each chromosome at a particular location called a **locus** (sing.) or **loci** (pl.). Different versions of the same gene are called **alleles**. If someone has the same version of a gene (the same alleles) on both of their homologous chromosomes, they have **homozygous alleles**. If, however, someone has two different versions of a gene (different alleles) on their homologous chromosomes, they have **heterozygous alleles**. For example, if on this person's chromosome 9 pair they have one allele for blood type A and one allele for blood type B, we would say that they are heterozygous for blood type (AB). If they have two alleles for blood type O, we would say that they are homozygous for blood type (OO).

Note

Explore human chromosomes

Mitosis

Somatic cells (AKA body cells) are replicated via the process of mitosis. This is where all new body cells come from. So, when you scratch yourself on something, mitosis is what makes new skin cells for healing that scratch.

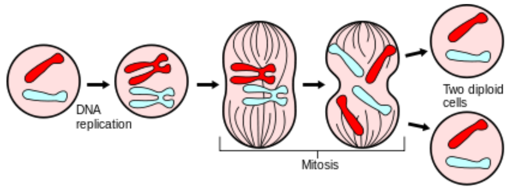

***Figure* 1.5.6** - *Mitosis*

Mitosis has 4 phases (note that DNA has already replicated when mitosis starts):

1) Prophase:

- the nuclear envelope disappears
- chromatin condenses and forms chromosomes
- the chromosomes move toward the equator of the cell

2) Metaphase

- the chromosomes are lined up along the equator of the cell

3) Anaphase

- the sister chromatids split up and move toward the opposite ends of the cell

4) Telophase

- the cytoplasm divides between the two cells
- the chromosomes turn back into chromatin

The result is two identical "daughter" somatic cells, each of which contains one chromosome from the "parent" cell and one replicated chromosome.

Here's a video that illustrates the process: mitosis in action.

Meiosis

Sex cells (eggs and sperm) are replicated via the process of meiosis. For human females this process occurs and is completed before birth, but for males meiosis begins at puberty and continues throughout their lifespans. Meiosis is more complicated than mitosis in that it has two "cycles".

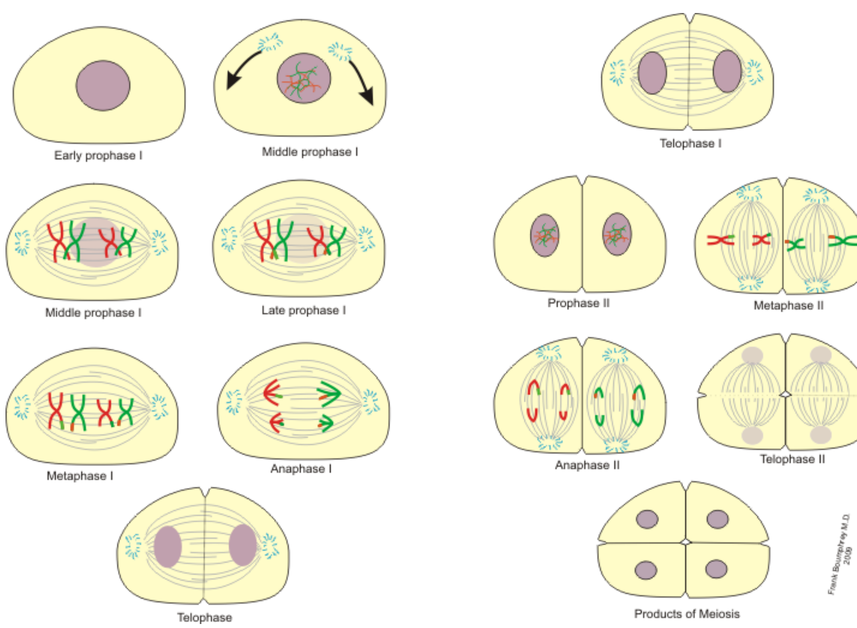

***Figure* 1.5.7** - *Meiosis*

1) Prophase 1

- chromatin condenses and forms chromosomes
- DNA is exchanged between homologous chromosomes. This is called homologus **recombination**. Recombination is an important source of genetic variation.
- the chromosomes start to line up at the equator of the cell

2) Metaphase 1

- the chromosomes are lined up along the equator of the cell

3) Anaphase 1

- the homologous chromosomes move toward the opposite ends of the cell

4) Telophase 1

- the cytoplasm divides between the two cells
- the chromosomes uncoil and turn back into chromatin

5) Prophase 2

- nuclear envelope disappears
- chromatin condenses into chromosomes
- the chromosomes start to line up at the equator of the cell

6) Metaphase 2

- the chromosomes are lined up along the equator of the cell

7) Anaphase 2

- the sister chromatids split apart at the centromeres and move toward the opposite ends of the cell

8) Telophase 2

- chromosomes turn back into chromatin
- the cytoplasm divides between the two cells

Here's a video that illustrates the process: meiosis in action

Errors during mitosis and meiosis

***Figure* 1.5.8** - *The karyotype of an individual with Down syndrome*

The chromosomes separate during meiosis 1 and the sister chromatids separate in meiosis 2 and mitosis. If this proceeds normally, it's called **disjunction**. If the separations occur abnormally, it's called **nondisjunction**. What results is an abnormal number of chromosomes (either too many, AKA trisomy OR too few, AKA monosomy).

Some of the more familiar nondisjunctions include:

Down Syndrome - trisomy of chromosome 21 (a karyotype of this is to the right)

Klinefelter Syndrome - extra X chromosomes in males (ex. XXY)

Turner Syndrome - lacking an X chromosome in females (XO)

1.6: Mendelian Genetics

In the previous section, we explored the mechanisms of biological variation and evolution at the most fundamental level - cells and DNA. In this section, we are going to look at how genetics functions for individuals. This field of genetics is often called Classical or Mendelian Genetics. It focuses on how various traits are passed from one individual to the next.

Some working vocabulary

- **Locus** (sing.) and **Loci** (pl.): the specific position of a gene on a chromosome
- **Gene**: a discrete unit of a DNA sequence that codes for a protein (or polypeptide) or for a characteristic, process, or trait
- **Allele**: alternate forms of a gene at a given locus (ex. T and t)
- **Genotype**: the genetic makeup of an individual
- **Phenotype**: the outward expression of the genotype, as affected by the environment and culture of an individual
- **Dominant allele**: an allele that masks the effect of other alleles in the phenotype (ex. in the case of Tt, T masks the effect of t)
- **Recessive allele**: an allele that is masked in the phenotype unless present in a double dose (ex. in the case of tt, there is no T to mask the effect of t)
- **Codominant allele**: both alleles are expressed in the phenotype (ex. in the ABO blood types, there are three alleles (A,B,O); A and B are codominant alleles)
- **Homozygous**: two of the same alleles at a given locus on homologous chromosomes (ex. TT or tt)
- **Homozygous dominant**: both alleles are the dominant allele (ex. TT)
- **Homozygous recessive**: both alleles are the recessive allele (ex. tt)
- **Heterozygous**: two different alleles (ex. Tt)

Note: Capital letters are usually shorthand for the dominant allele and lower-case is usually shorthand for the recessive allele when discussing Mendelian genetics.

Traits

Traits come in two types: Simple (also called Mendelian or discrete traits) and complex (sometimes called *continuous* or quantitative traits).

Simple traits

These are either/or traits (they usually have 2 phenotypes):

- The trait is either present or absent (e.g., hairy pinna).
- or the trait is one state or the other (e.g., attached or unattached earlobes: see image).
- It's controlled by one gene, which has one effect.

They are biologically (genetically) determined:

- They cannot be changed.
- There is little to no influence from the environment.
- They have a finite number of genotypes, usually very small. For example, 1 trait with 2 options (T and t) = 3 genotypes (ex. TT, tt, Tt).

There are approximately 4000 traits identified as discrete or simple traits of inheritance. Some additional examples include:

- Soft vs. flaky earwax
- Widow's peak
- Blood type
- Dimples
- Chin cleft (Figure 1.6.1)

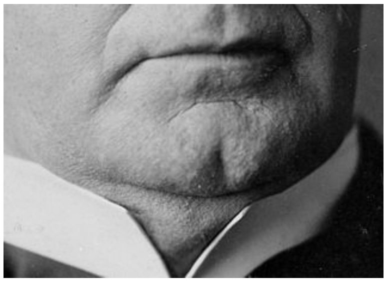

Figure $1.6.1$ - *Cleft chin*

Complex traits

- These traits have a continuous distibution (e.g., height: there are people ranging from short to tall, not just short and tall).
- The phenotype is the result of two factors; the number of loci involved and environmental influence (this includes culture).
- The trait is influenced by more than one gene; this trait is referred to as **polygenic**).
- Depending on the number of genes involved, there can be many genotypes. The more genes that are involved, the finer the genotype categories until they converge into a continuous distribution.
  - 1 gene = 3 genotypes
  - 2 genes = 9 genotypes
  - 3 genes = 27 genotypes
  - 4 genes = 81 genotypes
- It's often difficult to try to divide them into categories due to an infinite number of phenotypes

The opposite of this, where one gene has multiple effects, is called **pleiotropy**.

Due to the large role that the environment plays in complex traits, we have a statistical concept in genetics called heritability. **Heritability** is the proportion of the total variation observed in the population that can be attributed to genetics rather than to the environment.

Gregor Mendel and his Peas

For simple traits, it is easy to trace patterns of inheritance and use them to show how traits are passed on from one generation to the next. Charles Darwin thought that traits were passed down by "**blending**": each parent contributes equally to the offspring, and these contributions are mixed together and then halved at each successive generation (Figure $1.6.2$).

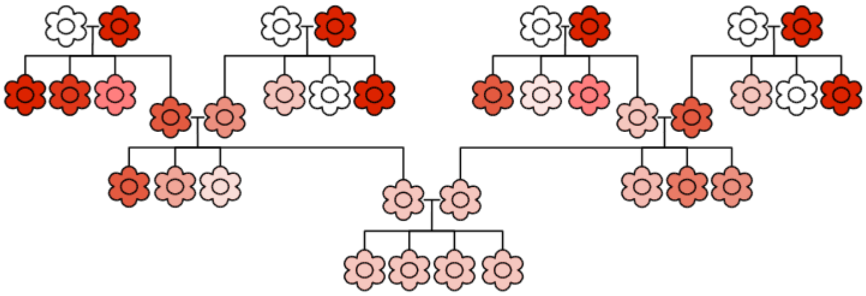

Figure $1.6.2$***:*** *Blending inheritance*

However, there was a contemporary of his that Darwin didn't know about, a monk named Gregor Mendel (pictured below), who figured out something important about simple traits and genes. Mendel is famous for a series of experiments that he completed with pea plants (between about 1856 and 1868) and the paper that he wrote about it (*Experiments with Plant Hybrids*). Unfortunately, despite the fact that Mendel published this work in 1865, it was relatively unknown until 1900. What he concluded was that genetic information is inherited in discrete units (he called them "factors", we call them "genes"). His work demonstrated that inheritance is non-blending or "**particulate**".

Figure **1.6.3** - *Gregor Mendel*

Mendel's pea experiments

Mendel first noticed that pea plants have seven simple traits:

1. Seed shape and color
2. Cotyledon color
3. Flower color
4. Pod shape
5. Pod color
6. Location of pods and flowers on the stem
7. Plant size

He also noted that when one selectively bred the plants with the various traits together, he could predict the ratios of offspring characteristics. For example, he noticed that when he bred pure-bred plants with violet flowers with those with white flowers, the first generation (F1) all had violet flowers. If blending inheritance was functioning, one would expect all of the flowers to be a pale violet, halfway between the original violet and white.

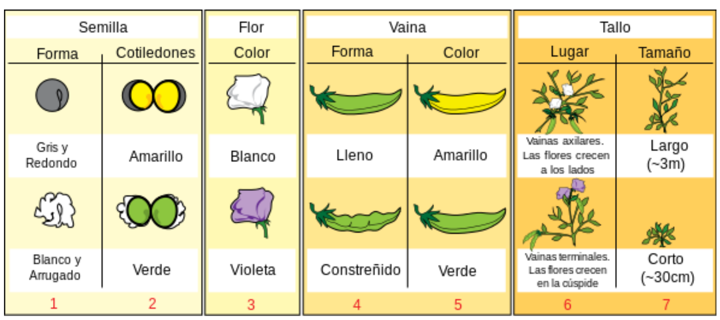

Figure **1.6.4** - *Mendel's seven traits*

Then when he took those F1 violet-flowered plants and bred them together, the second generation (F2) had a ratio of 3:1 violet to white flowers (there were still no pale-violet hybrids). This phenomenon was consistent across the pea plants' other six traits.

He determined that this is what was going on:

- The pure-bred violet plant was homozygous for its violet allele (BB).
- The pure-bred white plant was homozygous for its white allele (bb).
- So, when the two plants were crossed -- all of the offspring (F1) were heterozygous (Bb).
- And, when the heterozygous (Bb) offspring were crossed, this was the result: the genotype is 1 BB: 2 Bb: 1 bb and the phenotype is 3 violet: 1 white.

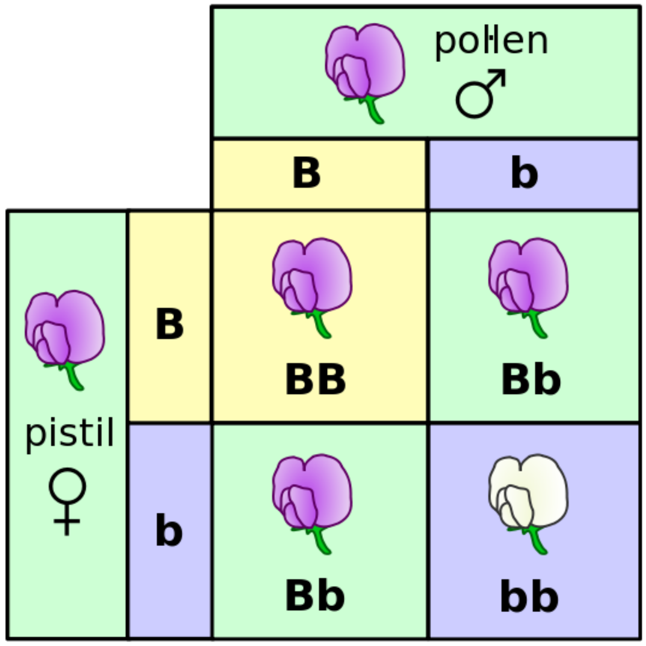

***Figure 1.6.5** - A Punnett square of pea flowers*

Punnett squares

This diagram in Figure 1.6.5 is called a Punnett square (after an early 20th c. English geneticist named Reginald Punnett). They're really pretty simple to construct. One just puts the alleles of each parent (one parent on the top and the other down the side) and then you fill in the boxes of what the offspring will be. In order to devise the ratios of the various genotypes and phenotypes, just count the number of boxes of each.

For further information on how to construct Punnett squares, go here or watch this video from Bozeman Science.

Mendel's very thorough experiments (some estimates say that he bred approximately 29,000 pea plants) lead him to write these four postulates.

Mendels' postulates

1. Genetic characteristics are controlled by genes that exist in pairs in individual organisms.
   - The pairs of genes that he's referring to are those on each pair of homologous chromosomes.
2. When an individual has two different genes for a particular trait, only one is expressed and is dominant to the other, which is recessive.
   - In other words, when an individual has a T allele and a t allele, the T allele will mask the expression of the t allele. Therefore, the phenotype expressed will be that of T.
3. During the formation of gametes (AKA sex cells, sperm and eggs), the genes separate, or segregate, randomly so that each sex cell receives one or the other with equal likelihood.
   - In other words, the offspring have an equal likelihood of getting a particular gene from one parent or the other.
   - This is also known as "Mendel's Law of Segregation".
4. During the formation of gametes, segregating pairs of genes assort independently of each other.
   - In other words, the segregation of any particular pair of genes does not affect the segregation of any other pair.
   - This is also known as "*Mendel's Law of Independent Assortment*"

Some examples of inheritance patterns in humans

Autosomal dominant traits

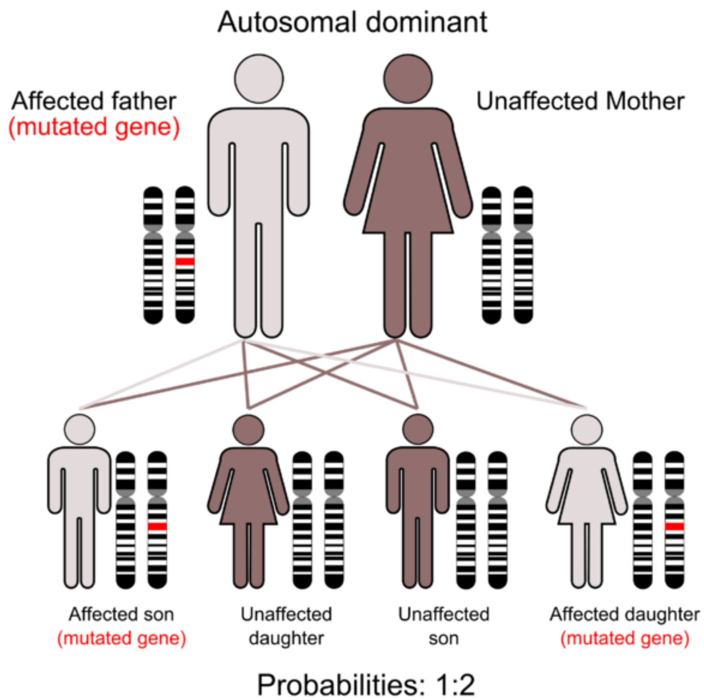

Figure 1.6.6 - Autosomal dominant inheritance

- An individual only has to have one copy of the allele in order to exhibit these traits.
- If an individual has the trait, then at least one of their parents has the trait.
- Both males and females are affected equally and should be capable of transmitting the trait.
- There is no skipping of generations.
- If one of the parents has it, then on average, 50% of the children will show the trait.

Examples of this include:

Huntington's disease

Neurofibromatosis-1

Autosomal recessive traits

- An individual needs both recessive alleles to express the trait
- Heterozygotes are considered to be "carriers"
- Both males and females should be affected equally and should be capable of transmitting the trait.

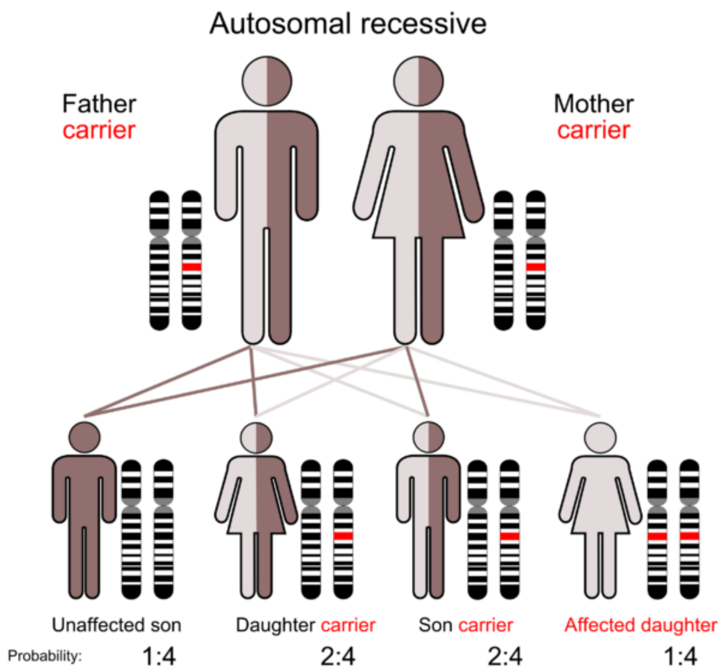

Figure 1.6.7 - *Autosomal recessive inheritance*

Examples of this include:

Cystic fibrosis, sickle cell anemia, and Tay Sachs disease

Sex-linked traits

- ***Remember*** that all females have two X sex chromosomes (XX) and males have one X and one Y sex chromosome (XY)
- These traits are inherited on the sex chromosomes (X and Y)
- There have different rates for males and females

There are three types:

1. X-linked dominant
2. X-linked recessive
3. Y-linked

X-linked dominant

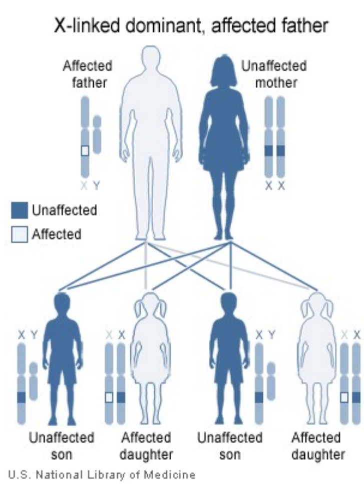

Figure 1.6.8 - *X linked dominant inheritance*

- Both males and females will express the trait if they possess at least one copy of the allele.

An example of this is:

Incontinentia pigmenti (IP)

X-linked recessive

- For females, they need two copies of the allele to express the trait, but only one to be a "carrier".
- For males, they need only one copy of the allele to express the trait. They will pass the allele down to all of their daughters.

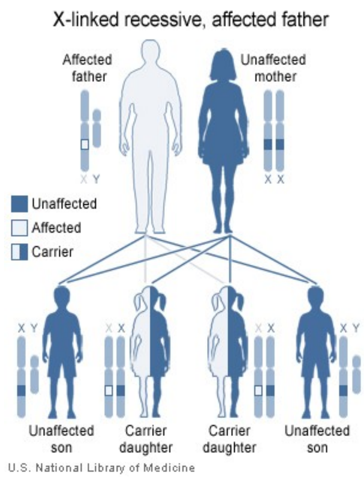

***Figure* 1.6.9** - *X linked recessive inheritance*

Examples of this include:

Red-green colorblindness and Hemophilia A

Y-linked

- No female will carry or express the allele (because they don't have a y chromosome)
- All sons will carry and express the allele (because they must inherit a y chromosome from their father)

An example of this is:

Hairy pinna

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1.7: Modern Synthesis

The Modern Synthesis incorporates data from multiple scientific disciplines: biology, the natural sciences, genetics, paleontology, and paleoanthropology. While the basis for evolutionary theory was established by the beginning of the twentieth-century, debate continued as to whether natural selection or mutation was more important in evolution. In the 1930s, these two points of views came together to form the basis of the modern synthesis. Fisher, Haldane, and Wright developed mathematical models that became the foundation of population genetics, which studies the frequency of alleles, genotypes, and phenotypes in populations (Miller 2011: 321). However, it was Theodosius Dobzhansky that married theoretical modeling and empirical research in his seminal work, Genetics and the Origin of Species (1937) and signals the start of the Modern Synthesis (Artmann 2006). Biologist Ernst Mayr was another major contributor to the development of the modern synthesis. His work on the isolating mechanisms of speciation led to new insight into the evolution of new species. Mayr's Systematics and the Origin of Species (1942) is one of the key works of the Modern Synthesis.

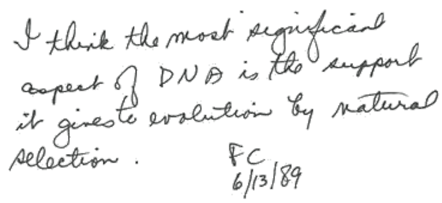

***Figure* 1.7.1** *- Note by Francis Crick.*

A New Definition

Emerging from the work of scientists of the Modern Synthesis, we know that evolution is a two-step process (Miller 2011: 85):

1. The production and redistribution of variation, and
2. Natural selection acts on variation resulting in differential reproduction among individuals in a population.

A **population** is a group of individuals from which mates are usually found. Sometimes this is referred to as a **breeding population**. All members of a population share a **gene pool**, which is all of the genes found among the individuals of the population.

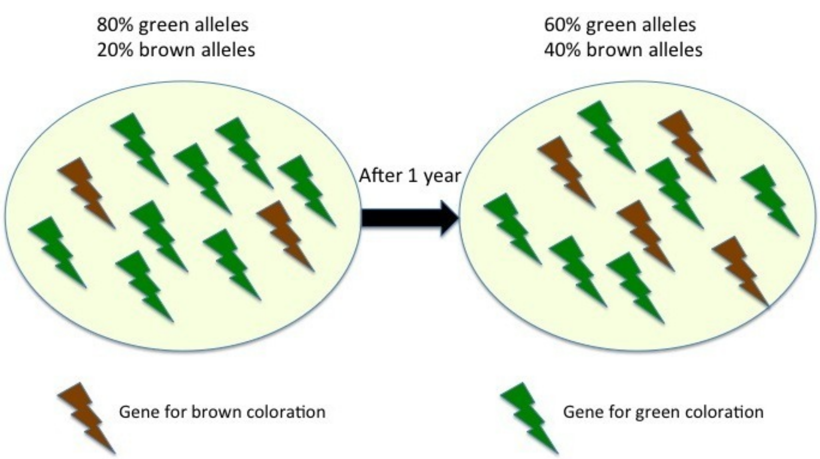

***Figure* 1.7.2** *- Graphic of microevolution. Modeled on University of California Museum of Paleontology's Understanding Evolution (evolution.berkeley.edu)*

Scientists can study variation in a gene pool and differential reproduction in populations to determine **allele frequencies**, which is the frequency of an allele relative to that of other alleles of the same gene. Changing allele frequencies within a population from one generation to the next is the definition of evolution; specifically, this is **microevolution. Macroevolution** is change that occurs after many generations (hundred or thousands); e.g., **speciation**, which is the evolution of a species into a new species. "Macroevolution encompasses the grandest trends and transformation in evolution, such as the origin of mammals and the radiation of flowering plants (Evolution 101, 2015). Macroevolutionary events are reconstructed using data from living organisms, geology, and fossils. These are generally represented in a graphic form called a **phylogentic tree** (pictured below). Phylogenetic trees are a visual representation of proposed evolutionary relationships. They help researchers organize data. To learn more about phylogenetic trees check out Reading a Phylogenetic Tree.

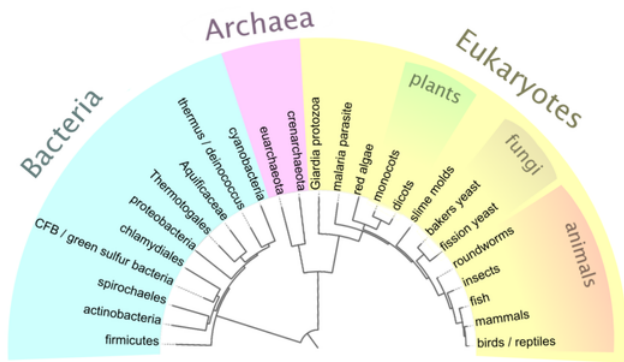

***Figure* 1.7.3** - *Simplified phylogenetic tree*

Step 1: Production and Redistribution of Variation

As we know, production and redistribution of variation is the first step of evolution. There are several factors involved in the production and redistribution of variation: 1. Mutation 2. Genetic drift 3. Gene flow, and 4. Recombination. These factors, along with natural selection, which is the second step of evolution, are frequently referred to as the **forces or mechanisms of evolution**.

Mutation

Mutation is a random change in the genetic coding and is the only new source of genetic material. Mutations occur during the DNA replication process. In an evolutionary sense, it is only mutations that occur during meiosis (replication of sex cells) that are hereditary. Many mutations do not have detrimental effects to the individual, but some do. If the mutations are extreme, pregnancy often results in spontaneous abortion (miscarriage). However, mutations provide a necessary pool of genetic variation in a population.

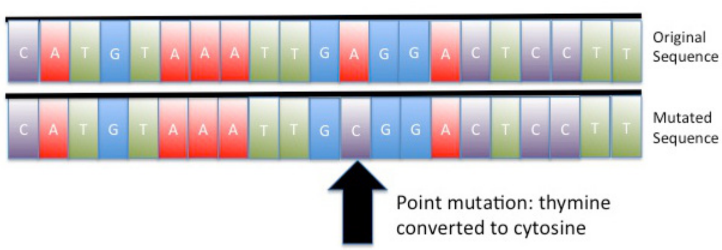

***Figure* 1.7.4** - *Illustration of a point mutation*

There are different types of mutations. The first is a **point mutation**, which is a small change in the DNA sequence. Point mutations may be **synonymous point mutations or silent mutations**, which means that while the codon is altered the same amino acid is produced, or **nonsynonymous point mutations**, which result in the production of a different amino acid that can have a negative effect on the individual. For instance, sickle cell anemia results in a point mutation where "…a mutation on human chromosome 11 converts a GAG codon into a GTG codon. The GAG codon is encoded to produce the amino acid valine, whereas the GTG codon is encoded to produce glutamic acid. This substitution results in sickle cell anemia…" (Larsen 2008: 93).

Frameshift mutations occur when one or more nitrogenous bases are inserted into or deleted from the DNA sequence. The insertion or deletion causes the reading of the gene to be altered or stopped. It results in the production of a nonfunctioning protein.

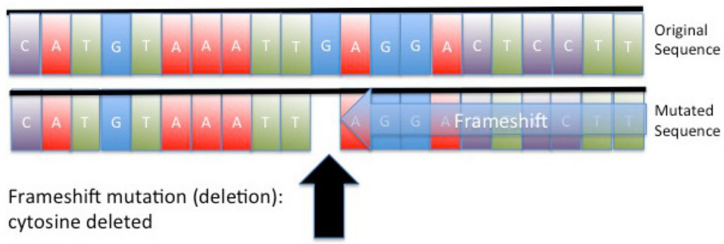

Figure 1.7.5 - *Illustration of a deletion mutation*

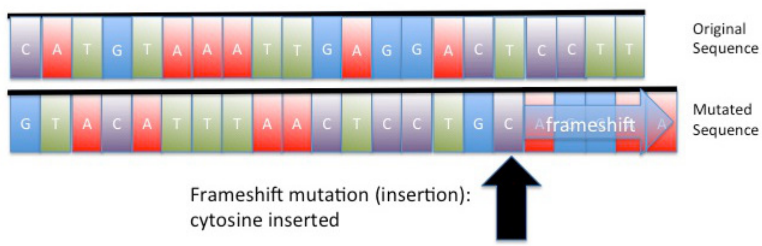

Figure 1.7.6 - *Illustration of an insertion mutation*

Transposable elements are mutations that occur when pieces of DNA copy themselves into new areas of chromosomes. If this occurs in a non-coding segment of the DNA then there are little to no effects on the individual. If it transposes to a coding segment of DNA then serious consequences can occur. In extreme cases, entire chromosomes may be copied (a trisomy) or deleted (a monosomy).

Mutations may have no known cause. These are called **spontaneous mutations**. Mutations caused by environmental factors are called **induced mutations**.

Genetic Drift

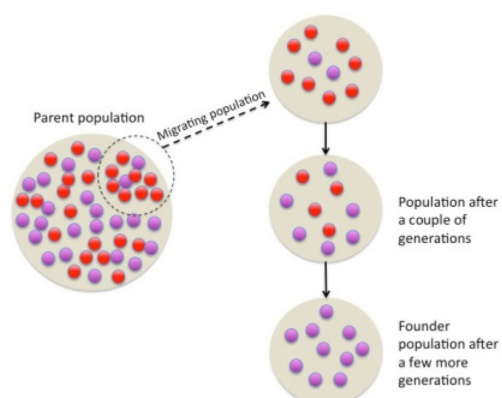

Figure 1.7.7 - *Illustration of founder effect*

Genetic drift is the "…chance variation in allele frequency in small populations" (Gould 2006:1036). This can happen in a couple of ways: founder effect and bottleneck effect (or population bottleneck). **Founder effect** can occur if a small group separates from its parent group and settles elsewhere. Geographic isolation and endogamous marriage (human marriage pattern where mates are chosen from within a specific group, narrowing the gene pool) or mating practices restrict the gene pool, resulting in a lack of variation in comparison to the original parent population. If an allele is rare in the parent population, the small breeding population of the new group creates an environment whereby the rare allele can become common.

There are numerous examples of the founder effect among human populations. These include,

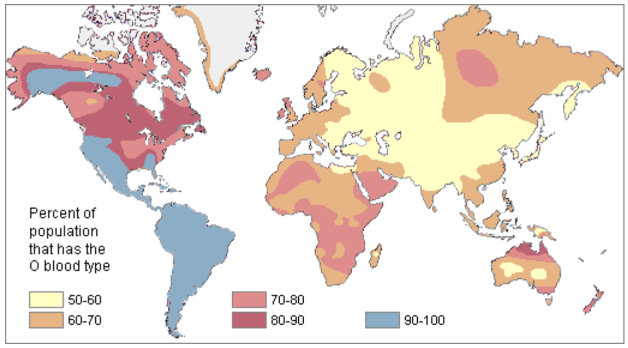

Figure \(\PageIndex{8}\) - Map of blood group O

- Huntington's Disease in Afrikaner populations in South Africa and among Venezuelans living near Lake Maraciabo,
- Prevalence of O blood type in Native Americans
- Ellis-van-Creveld syndrome (polydactyly) in Amish communities, and
- The Blue People of Kentucky (learn more about the Blue People www.indiana.edu/~oso/lessons/Blues/TheBlues.htm).

Bottleneck effect occurs when a population is drastically reduced in size due to some disaster, e.g., natural disaster, habitat destruction, or disease, leaving the surviving population with different allele frequencies as the original population. Four human population bottlenecks all related to climatic events have been identified. The most severe occurred about 70,000 years ago when a supervolcano erupted in Sumatra. It is estimated that only 5000 females survived in Africa (Ambrose 2003).

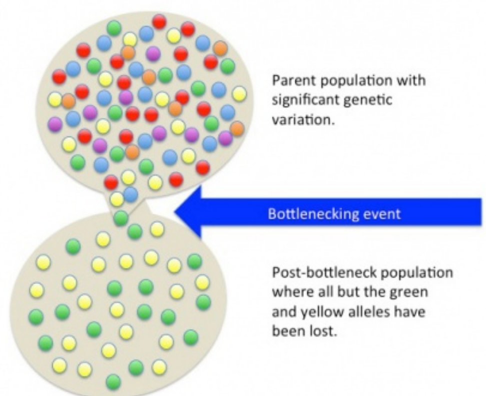

Figure 1.7.9 - Illustration of the bottleneck effect

Gene Flow

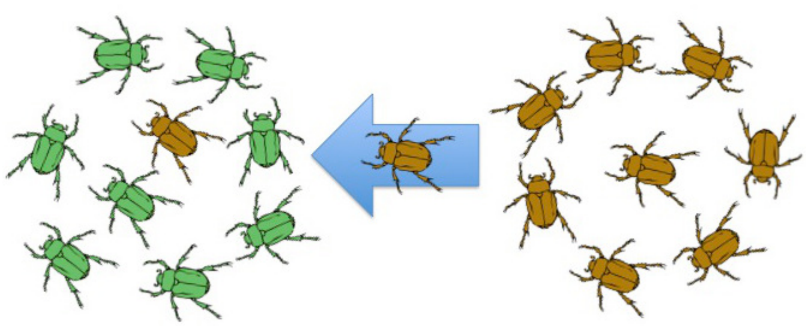

Figure 1.7.10 - Illustration of gene flow.

Gene flow, also called **admixture** or migration (in reference to people), is the exchange of genetic material between populations (Miller 2011). For humans, gene flow generally occurs when people move from one location to another; however, in the modern world it is not out of the realm of possibility that someone's genetic material could move with the actual human being leaving their hometown. It should also be noted that migration does not always result in gene flow. For gene flow to occur interbreeding must happen. Human populations have exchanged genetic materials for millennia, helping to explain why there is only one human species.

Gene flow effects evolution in a couple of important ways (Evolution 101, 2015): • With the introduction and reintroduction of genes to a population its genetic variation is increased, and • The movement of genetic material can make distant populations genetically similar to one another, which reduces the chance of speciation.

Recombination

Recombination, or crossing over, can occur during meiosis. As the term implies, segments of chromosomes are exchanged between non-sister chromatids. This creates new combinations of genes that are not found in either parent (Speer 2003).

Step 2: Natural Selection

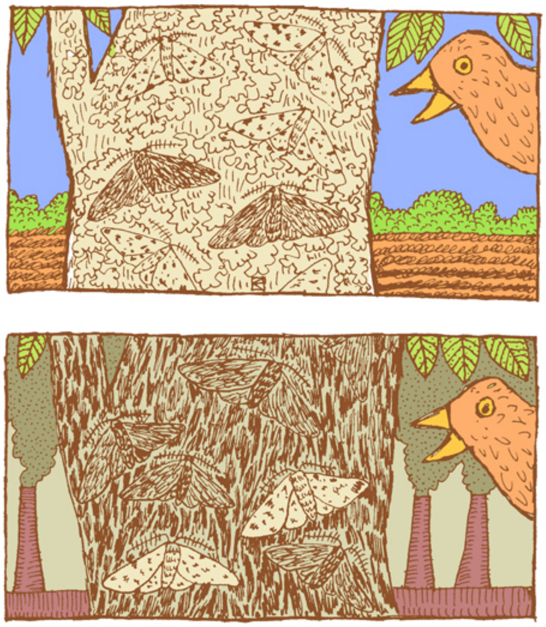

***Figure* 1.7.11** - *Peppered moths.*

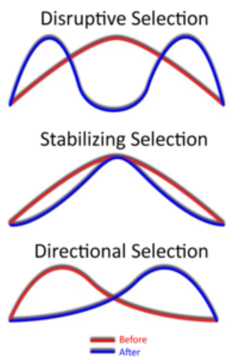

***Figure* 1.7.12** - *Types of selection.*

Once variation is produced in some combination of the above processes, natural selection goes to work, causing directional change in allele frequency

related to environmental conditions that may result in evolutionary change, i.e., speciation. Shifts in allele frequency are called **adaptation**. In phrasing it this way, it sounds like natural selection works consciously, but it does not. Natural selection is a process that is mindless and mechanistic. Perfection and progress are not goals. It can only act on those variants that are present in a population.

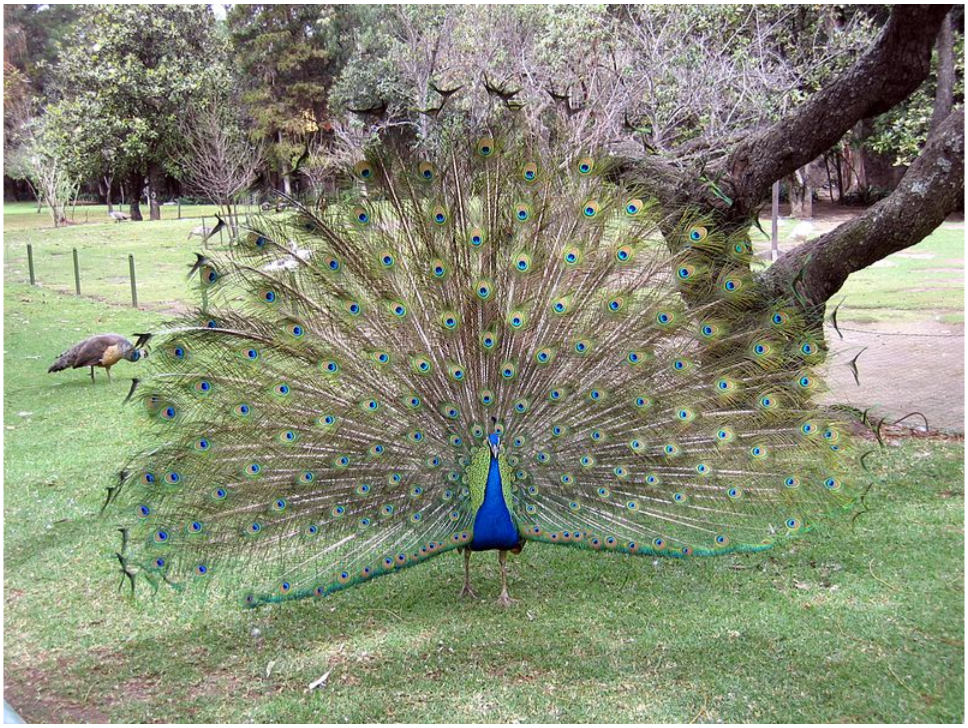

***Figure* 1.7.13** - Male peacock display.

Darwin concluded, "…individuals with advantageous characteristics…survive in higher numbers and produce more offspring than members of a population lacking advantageous characteristics" (Larsen 2008: 96). This is referred to as **differential reproduction** or **fitness**. Specifically, fitness is defined by genotypes—some genotypes confer an advantage to an individual allowing that individual to reproduce at a greater frequency than another individual, characteristics that are inherited by their offspring. It could be something like beak shape that allows a bird to exploit resources better than other birds (think Darwin's finches) or the color of wings that either hide or expose the peppered moth to predators (watch youtu.be/sVVldxxbWig for the full explanation) or a coloring, like the plumage of a male peacock, that attracts mates (this is referred to as **sexual selection**, which is a special case of natural selection which refers to an individuals ability to attract and copulate with a mate) that lead to differential reproduction.

There are three types of selection: disruptive, stabilizing, and directional selection. With disruptive selection, both homozygotes (the phenotypic extremes) are selected for while with directional selection only one of the homozygotes is selected for. Disrupting selection may result in a speciation event. Stabilizing selection refers to selection for the heterozygote, resulting in decreasing genetic diversity within the population.

If you would like a bit more on the types of selection, check out Bio.edu: Stabilizing selection (http://www.brooklyn.cuny.edu/bc/ahp/LAD/C21/C21_Stabilizing.html) Disruptive selection (http://www.brooklyn.cuny.edu/bc/ahp/LAD/C21/C21_Disruptive.html) Directional selection (http://www.brooklyn.cuny.edu/bc/ahp/LAD/C21/C21_Directional.html)

Species and Speciation

Mayr proposed the most commonly referenced definition of species (1942; quoted in Provine 2004), "Species are a group of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." This definition is often referred to as the **biological species concept**. A key factor is that a species actually or potentially breeds in nature. However, this definition can be difficult to apply; e.g., organisms that reproduce asexually or organisms that form hybrids (carrion crows and hooded crows sometimes interbreed—are they one species or two species?). The biological species concept falls apart when applied to the fossil record, as it is impossible for scientists to observe the breeding behaviors of extinct organisms. Because of this, fossil species are called **paleospecies** and can cover long periods of time. Paleontologists and paleoanthropologists use comparative analysis with contemporary species that are closely related to determine whether variation seen in fossil specimens is **intraspecific** (differences within a species due to age and sex) or **interspecific** (differences due to reproductive isolation). It is important to remember that the species or paleospecies name is a classificatory tool used in the sciences. It helps scientists organize information and communicate more easily with one another.

Speciation is "…the process by which a new species evolves from an earlier species (Jurmain et al 2013: 105). This idea is one of Darwin's five theories, specifically those of common descent and multiplicity of species, whereby new species arise from earlier species.

Simsonian Evolution

Just for fun, check out how The Simpsons explain evolution: www.youtube.com/watch?v=faRlFsYmkeY

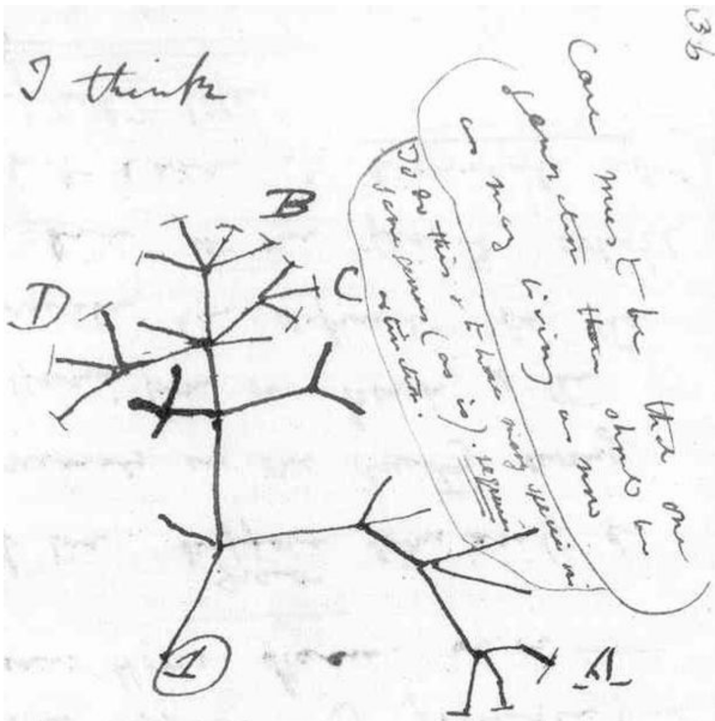

***Figure* 1.7.14** - *Darwin's first tree.*

Explore (optional)

If you would like to read more about the concepts introduced on this page, check out the following web sources:

What is evolution? A short essay by Laurence A. Moran exploring the definition of evolution. (bioinfo.med.utoronto.ca/Evolu...Evolution.html)

Evolution is a Fact and a Theory. Another short essay by Moran explaining how evolution is both a fact and a theory. (bioinfo.med.utoronto.ca/Evolu...nd_Theory.html)

Why is evolution controversial anyway? A short PBS video discussing the controversy of evolutionary theory. You will need Quicktime or RealPlayer to watch this video. This page has several videos on it—look for the video entitled Why is evolution controversial anyway? (http://www.pbs.org/wgbh/evolution/educators/teachstuds/svideos.html)

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1.8: Modern Human Variation

One of the most striking things about humans is the huge range of biological variation we have as a species. In the previous section, we explored the mechanisms of change involved in the evolution of populations (mutation, migration/gene flow, genetic drift, and natural selection). In this section, we'll look at how those affect human populations to create human diversity.

Polymorphisms

A **polymorphism** is when a gene has at least two different alleles (and each allele is in more than 1% of the population).

ABO blood type is a perfect example of a polymorphism, which, you will recall, means there are two or more alleles at a locus. In the ABO blood group there are three alleles (A, B, and O) prevalent in most human populations. There are a few populations in the world which are not polymorphic. The O allele occurs in almost 100% of South American indigenous populations and is remarkably high in aboriginal groups in northern Australia. This is most likely due to genetic drift. When alleles vary geographically, they have a **clinal** distribution. As you can see in the maps below, B is more common in Europe and Asia, and A is found in high numbers in Asia and central Africa.

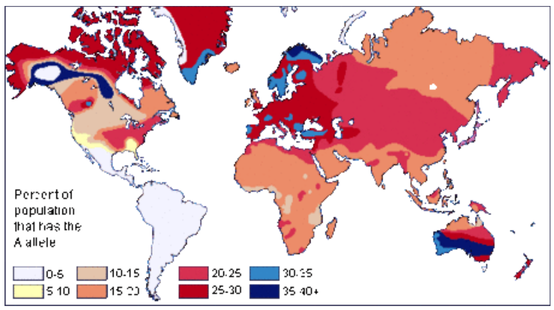

***Figure* 1.8.1** - *Map of blood group A*

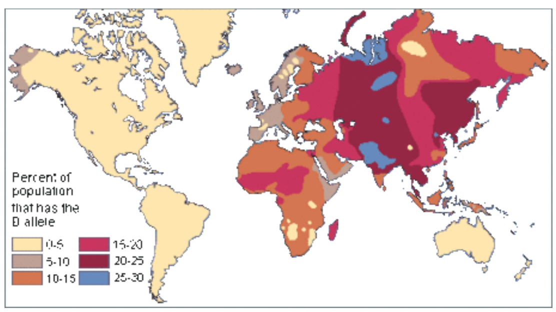

***Figure* 1.8.2** - *Map of blood group B*

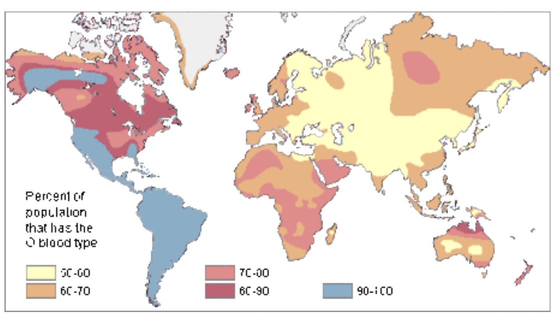

***Figure* 1.8.3** - *Map of blood group O*

You can learn more about the ABO blood group from the American Red Cross.

Using polymorphisms: clines and migration

If you know the clinal distribution of a polymorphism, you can use the movement of the alleles as a proxy for the movement of people.

For example, the map below shows the distribution of a group of genes called Haplogroup F (found on the Y chromosome) throughout the Middle East, Europe, and Asia. Presumably the distribution of the genes follow the movement of peoples as they dispersed from India outward.

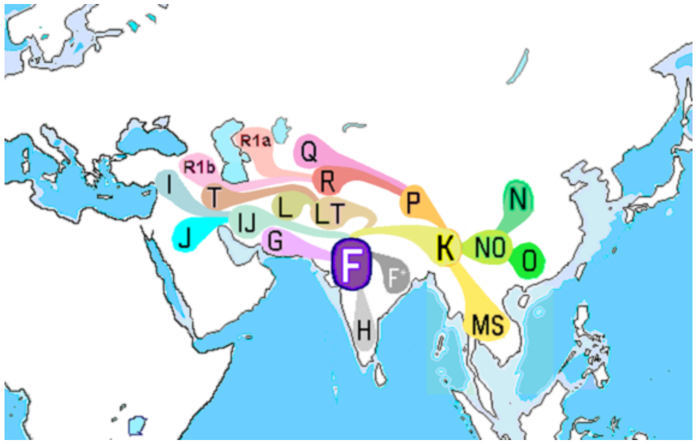

***Figure* 1.8.4** - *Haplogroup F (Y-DNA)*

Natural selection and polymorphisms

While some clinal distributions are due to migration (gene flow), others have been shaped by natural selection.

Lactose tolerance

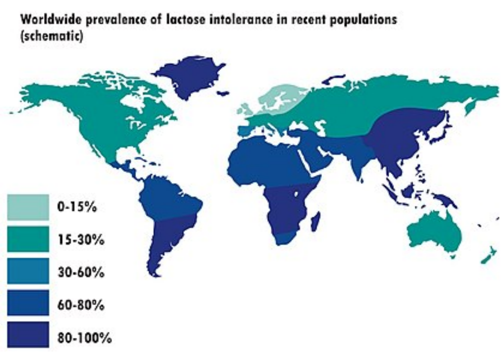

***Figure* 1.8.5** - *Worldwide prevalence of lactose intolerance in recent populations.*

The original human condition (found in most southern European, Asian, and African populations) is an inability for adults to digest lactose, the primary sugar found in dairy products. This is known as lactose intolerance and it has a genetic basis. Lactose intolerance can be a particularly unpleasant condition for those who consume dairy products and cannot digest them. Symptoms include diarrhea and intestinal gas.

However, some populations of people have developed an ability to digest lactose.

This is how that came about:

- An individual (or individuals) in the population was born with a genetic mutation that allowed them to digest lactose.
- During the same time span, the population was domesticating dairy-producing animals, collecting milk, and consuming it.
- Those who could digest the lactose in the milk (and therefore had a good food source without the unpleasant side effects) had more children than those who could not digest the lactose.
- Those children inherited the gene for lactose tolerance from their parents and passed it down to their children, etc.

This is **biocultural coevolution** between the domestication of dairy-producing animals in those populations and an increase in the prevalence of the lactose tolerance gene. In other words, the biology of the people was affected by their cultural behaviors and vice versa.

Sickle cell anemia

Sickle cell anemia is a very serious genetic disease that affects the hemoglobin in the blood.

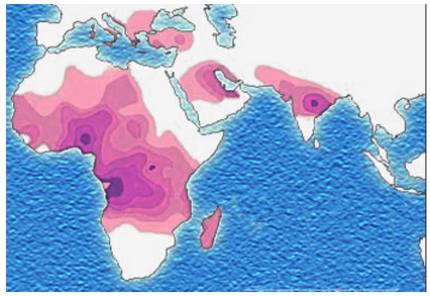

Figure **1.8.6** - *Sickle cell distribution*

There are two forms of the Hb (hemoglobin) allele: 1) HbA, which is for normal functioning hemoglobin, that which allows red blood cells to carry oxygen efficiently, and 2) HbB (sometimes written as HbS), which is for sickle cell anemia (the hemoglobin and red blood cells do not function normally).

So, as we learned before about alleles and genotypes, when there are two alleles, there are three genotypes. In this case, the genotypes and phenotypes are:

- HbA/HbA = homozygous person has totally normal hemoglobin and their blood transports oxygen perfectly.
- HbA/HbB = heterozygous person has "the sickle cell trait" and therefore is a genetic carrier, but usually has few to no associated medical problems.
- HbB/HbB = homozygous person has sickle cell anemia.

Sickle cell anemia is a good example of the interaction of biology, environment, and culture. It has a fascinating biological interaction with the infectious disease malaria, which in turn is associated with agricultural practices. It has been found that those with sickle cell trait, i.e., people with the HbA/HbB genotype, are less likely to get malaria. Malaria is a disease caused by a parasite, *Plasmodium*. This life-threatening disease is transmitted through the bites of *Anopheles* mosquitos. Symptoms include fever, headache, chills, and vomiting. In severe cases, anemia, respiratory distress, or death may occur. Malaria in sub-Saharan Africa is associated with the spread of slash-and-burn agriculture and irrigation.

To recap:

- those with HbA/HbA easily get malaria,
- those with HbB/HbB get sickle cell anemia,
- those with HbA/HbB have protection from malaria and not have sickle cell anemia,

This is called the **heterozygote advantage**, because the heterozygotes are better off than either one of the homozygotes. It's this advantage that keeps the HbB allele present in certain populations, which is an example of a **balanced polymorphism**.

Important note: Remember that this HbB advantage only exists in malarial environments. It is **environmentally specific**. In an area without malaria, there is no advantage to having the HbB allele and therefore, the frequency of that allele is lower in populations in non-malarial environments.

A little fun with malaria: Malaria the video game

Adaptations and adaptability

Humans have **biological plasticity**, or an ability to adapt biologically to our environment. An **adaptation** is any variation that can increase one's biological fitness in a specific environment; more simply it is the successful interaction of a population with its environment. Adaptations may be biological or cultural in nature. Biological adaptations vary in their length of time, anywhere from a few seconds for a reflex to a lifetime for developmental acclimatization or genetics. The biological changes that occur within an individual's lifetime are also referred to as **functional adaptations**. What type of adaptation is activated often depends on the severity and duration of **stressors** in the environment. A stressor is anything that disrupts homeostasis, which is a "condition of balance, or stability, within a biological system..." (Jurmain et al 2013: 322). Stressors can be abiotic, e.g., climate or high altitude, biotic, e.g., disease, or social, e.g., war and psychological stress. Cultural adaptations can occur at any time and may be as simple as putting on a coat when it is cold or as complicated as engineering, building, and installing a heating system in a building.

Types of Biological Adaptation

Acclimatization

This form of adaptation can take moments to weeks to occur and is reversible within an individual's lifetime no matter if it occurs when one is a child or an adult.

Short-term acclimatization can occur within seconds of exposure to a stressor. This type of response quickly reverses when the stressor is no longer present. Imagine stepping out of an air-conditioned building or car into a 90 degree day. Your body will quickly begin to perspire in an attempt to cool your body temperature and return to homeostasis. When the temperature declines, so will your perspiration. Tanning is another short-term response, in this case to increased UV-radiation exposure especially during summer months, which can occur within hours. Tans are generally lost during the winter when UV-radiation decreases.

Developmental Acclimatization

Developmental acclimatization occurs during an individual's growth and development. It's also called **ontological** acclimatization or developmental adjustment. Note that these cannot take place once the individual is fully grown. There is usually a "magic time window" of when the acclimatization can occur. This adaptation can take months to years to acquire.

A famous example of this is those who have grown up at high altitude vs. those who have moved to high altitude as adults. Those who were born at high altitude tend to develop larger lung capacities than do those who were not born at high altitude, but moved there later in life. However, developmental adjustment occurs in response to cultural stressors as well. Intentional body deformation has been documented throughout human history. The ancient Maya elite used cradle boards to reshape the skull. Foot binding in China, now an illegal practice, was considered an mark of beauty and enabled girls to find a wealthy spouse.

Genetics

Genetic adaptations can occur when a stressor is constant and lasts for many generations (O'Neil 1998-2013). The presence of the sickle cell allele in some human populations is one example. Keep in mind that genetic adaptations are **environmentally specific**. In other words, while a particular gene may be advantageous to have in one environment (AKA a genetic adaptation), it may be detrimental to have in another environment.

Human genetic adaptations and human variation

Skin color

Click on this link to watch a fantastic video explaining the interplay of skin color, UV, and vitamin D.

***Figure* 1.8.7** - *Inuit women*

Body size and shape

***Figure* 1.8.8** - *Young Maasai men*

There are two ecological rules, known as Bergmann's rule and Allen's rule, that explain the variation in size and shape of bodies and extremities using latitude and temperature.

Bergmann's rule: Warm-blooded animals tend to have increasing body size with increasing latitude (toward the poles) and decreasing average temperatures.

Allen's rule: A corollary of Bergmann's rule that applies to appendages. Warm-blooded animals tend to have shorter limbs with increasing latitude and decreasing average temperatures

When organisms are more compact, they tend to conserve heat (due to a high mass:surface area ratio). When organisms are more linear, they tend to lose more heat (due to a low mass:surface area ratio).

This has been applied to humans. The idea is that populations toward the pole tend to be shorter and have shorter limbs than do people on the equator.

For example, the Inuit people of Canada (pictured above) tend to be shorter than the Maasai people of Kenya (pictured below):

Race

Technically, a race is a biologically classifiable **subspecies**. So, when we are asking, "Do human races exist?", what we're really asking is, "Are there biologically classifiable subspecies in humans?".

Here's the American Anthropological Association's statement on race

and the American Association of Physical Anthropologists statement on race

What are they saying?

Basically:

- race is an arbitrary categorization, races are not biologically distinct groups (in other words, race is a cultural construct, not a biological one)
- while groups of people who have lived together for a long time may have some alleles in common (for example, those that code for skin color or hair color), there is more genetic variation within races than there is between races
- the concept of race has historically been a tool that some people use to subjugate others

Further explore the concept of race, its history, and human variation.

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CHAPTER OVERVIEW

II: Non-Human Primates

Learning Objectives

At the end of this unit, students will be able to:

- understand the classification of living things
- define the parts of Skeletal Anatomy
- identify shared primate traits
- understand the taxonomy of the living primates
- summarize Primate Ecology&Behavior
- identify some of the living primates: Strepsirhines; New World Monkeys; Old World Monkeys; Apes
- describe Fossils & Primate Evolution

In the second unit, students will examine skeletal anatomy, taxonomy, modern non-human primates, primate socioecology, and primate evolution.

Thuymbnail: Lémurien Propithèque de Verreaux. (CC BY 2.0; Jean-Louis Vandevivère).

2.1: Classification - Ordering the Natural World

As we learned in Unit 1, Carolus Linnaeus developed what is known as the Linnaean system of classification. This basic system is still used today, although it is focused on illustrating evolutionary relationships between organisms. This may sound familiar and it should---think phylogentic tree! Now we take a moment to look in more depth at classification.

Why do we bother with classification systems? Classification systems are important to help scientists organize the massive diversity of the natural world. It's a method that helps scientists from different countries talk about the natural world without confusion. Modern classification is considered a natural system representing real relationships between organisms. One thing to keep in mind when looking at classification systems is that it is basically a hypothesis about evolutionary relationships between species, which is why you may see different schemes as researchers may interpret data differently.

The Linnaean System

This hierarchical system organizes organisms into ever increasingly similar categories. Linnaeus' system has been modified from when he originally published *Systema Natura* in 1735. He published ten editions of the book, adding new levels to the hierarchy.

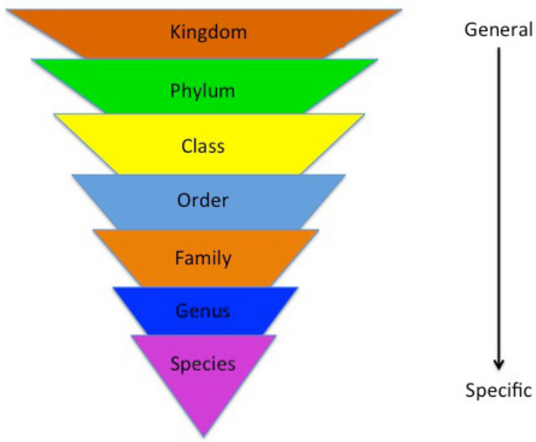

***Figure* 2.1.1** - *Classification diagram*

According to the Linnaean system, human beings are classified as follows (Larsen 2008: 36):

Category Level Common Characteristics

Kingdom	Animalia	mobile multicellular organisms that consume other organisms for food and develop during an embryo stage
Subkingdom	Eumetazoa	all major animals except sponges that contain true tissue layers, organized as germ layers, which develop into organs in humans
Phylum	Vertebrata	group of vertebrate and invertebrate animals that have a notochord, which becomes the vertebral column in humans and other primates
Superclass	Tetrapoda	vertebrate animals with four feet or legs, including fish, amphibians, birds, dinosaurs, and mammals
Class	Mammalia	group of warm-blooded vertebrate animals that produce milk for their young in mammary glands; they have hair or fur and specialized teeth
Subclass	Theria	group of mammals that produce live young without a shelled egg

Kingdom	Animalia	mobile multicellular organisms that consume other organisms for food and develop during an embryo stage
Order	Primates	group of mammals specialized for life in the trees, with large brains, stereoscopic vision, opposable thumbs, and grasping hands and feet
Suborder	Anthropoidea	group of primates, including monkeys, apes, and humans, but not prosimians; they have long life cycles and are relatively large-bodied
Family	Hominidae	group of anthropoids, including humans and great apes, and human ancestors; they have the largest bodies and brain sizes of all the primates
Genus	*Homo*	group of hominids including modern humans, their direct ancestors, and extinct relatives; they are bipedal and have large brains
Species	*sapiens*	modern and ancestral modern humans; they have culture, use language, and inhabit every continent except Antarctica
Subspecies	*sapiens*	modern humans alone

Rules of Classification

Taxonomy or systematics is the field that establishes the rules of classification. As established by Linnaeus, organisms are first classified by their physical similarities. Remember, today classification is interested in illustrating evolutionary relationships, so it is not enough simply to establish that there are physical similarities; it is important to try and understand how the similarities arose…was it because of a close common ancestor or some other reason.

To begin classification, researchers identify anatomical features that have the same function as that of similar structures in other species. Then they determine whether the similar features are due to a homology or analogy. A **homology** is a trait found in two or more different organisms that was inherited from a common ancestor. The more homologies shared by two organisms, the closer the genetic relationship. The structure of your arm, the wing of a bird, the fin of a whale, and the forelimb of lizard are examples of homologies. Confusing? Think of this as cousins who inherit the same trait from their grandfather (Understanding Evolution). These types of traits are called homologous structures or simply, homologies. Click here for another image.

However, not all similarities are homologies. An octopus has limbs, but the structure is not the same as the tetrapods referred to above. Octopus limbs evolved independently after they split from their shared ancestor with tetrapods. This type of similarity is called an **analogy** or analogous structure. How can analogous structures evolve in separate species? Analogies are a response to similar pressures. The Understanding Evolution website has a short animation that helps to explain this: evolution.berkeley.edu/evolibrary/article/0_0_0/similarity_hs_08.

In order to determine whether a trait is a homology or analogy, researchers have some criteria to help them make the determination:

- Do the bones have the same basic structure?
- Do the bones have the same relationship to other features?
- Is the development of the structure the same?

Researchers also try to distinguish whether or not structures are due to parallel evolution or convergent evolution. **Parallel evolution** refers to situations where organisms that are unrelated or distantly related have similar adaptations because of similar environmental pressures. When parallel evolution occurs "in distantly related [organisms] that are morphologically similar in overall appearance" (Armstrong 2002-2008) it is called **convergent evolution**. An example that will hopefully make this concept more clear comes from the plant world. *Cactaceae* (North American cactuses) and *Euphorbiaceae* (South American euphorbias are distant relatives that both have characteristics we attribute to succulents—thick stems, spines, and adapted to deserts, but they belong to different plant families).

***Figure* 2.1.2** - *Cactaceae:* Opuntia bigelovii

***Figure* 2.1.3** - *Euphorbiaceae:* Euphorbia aggregata ies

Some scientists use the terms interchangeably, making them even more confusing then they already are; this group of scientists proposes that what we are seeing are two different ends of a continuum. They suggest that we simplify terminology and call it convergence. To help make the distinction between 1) similarity due to a common ancestor and 2) similarities due to distantly related ancestors, some researchers use the term homology to refer to the former condition (#1 above) and **homoplasy** to refer to the latter (#2 above) (Armstrong 2002-2008).

Building Classifications

There are two basic schools of thought in constructing classifications or evolutionary relationships: Evolutionary systematics and cladistics. **Evolutionary systematics** is the traditional approach that relies on analysis of homologous characters (or traits), phylogeny, divergence, and adaptational level to establish evolutionary relationships. It arose out of the Modern Synthesis, in particular the work of Ernst Mayr, G. G. Simpson, and Thomas Cavalier-Smith, and has a time component to it. In more recent times, DNA sequences have been incorporated into the construction of evolutionary relationships.

Cladistics, or phylogenetic systematics, also reconstructs evolutionary relationships but only uses derived homologous characters. **Derived traits** are those characters that are different from the ancestor in form or function. An example of a derived trait for humans is the chin. **Ancestral traits**, which are sometimes referred to as primitive traits, are those characters inherited from the ancestor. For humans, the opposable thumb is an ancestral primate trait. Cladistic evolutionary relationships are presented in a cladogram and do not indicate time. Groups of organisms that share a common ancestor are part of **clade**.

Learn more about Reading Phylogenies and Cladograms from the Understanding Evolution web site.

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2.2: Primate Skeletal Anatomy

The study of bones is called **osteology**. It is necessary to have a basic understanding of the skeletal anatomy since the data used in the study of primate and human evolution is based on fossilized bones. The information presented here focuses on the human skeleton. Human beings have an **endoskeleton**, which means that the skeletal structure is on the inside of the body. The endoskeleton grows along with the rest of the body. Endoskeletons are lighter than exoskeletons (skeletal system on the outside of the body), which allowed for the evolution of large vertebrate animals. The endoskeleton is comprised of bone. Bone has three structural parts:

1. Compact bone (periosteum): dense outer layer
2. Spongy bone: light, softer inner layer
3. Marrow: fills the inside core and makes red and white blood cells.

For the skeletal system to work properly it must have ligaments that connect the bone at the joints, muscles connected to the bones with tendons that allow for movement of the bone, and cartilage that fills the spaces between the bones, preventing them from scraping against one another.

Human infants have 270 bones, several of which fuse together during growth so that adult humans have 206 bones. The skeleton is divided into two categories: the axial skeleton and the appendicular skeleton. The **axial skeleton** is comprised of the vertebral column, ribs, sternum, and skull.

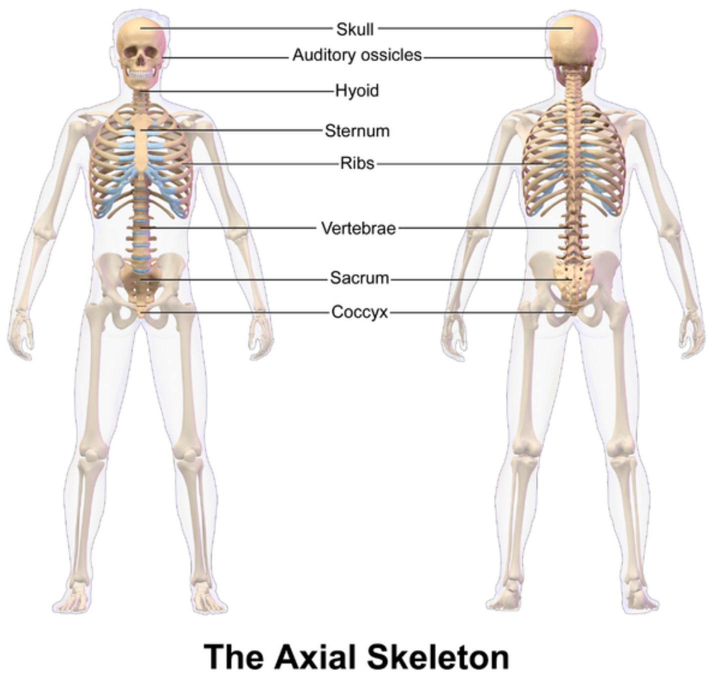

Figure 2.2.1 *- Axial Skeleton*

The human skull has a number of bones. These bones were seperate at birth and then fuse together as an individual ages.

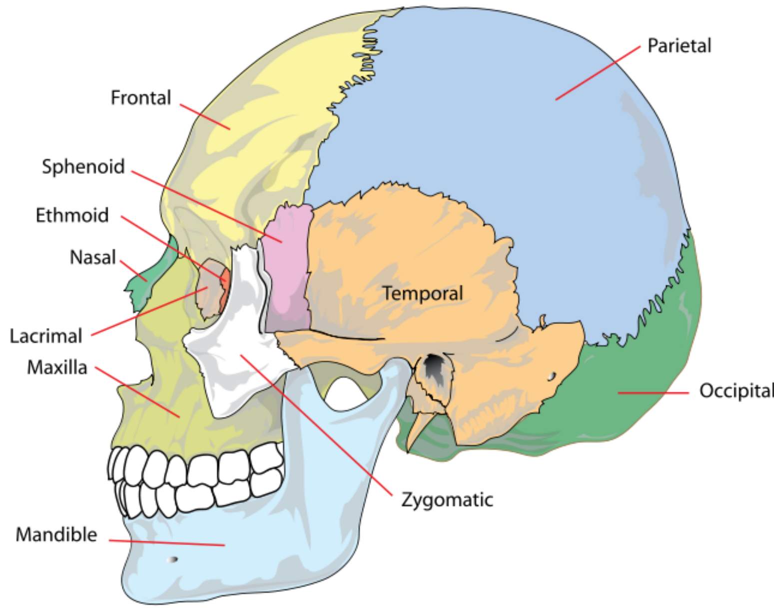

***Figure* 2.2.2** - *Human skull bones (simplified)*

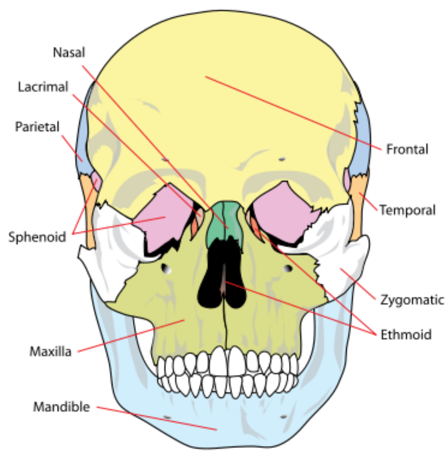

***Figure* 2.2.3** - *Human skull front bones (simplified)*

The **appendicular skeleton** is composed of the shoulder girdle, upper limbs, pelvic girdle, and the lower limbs.

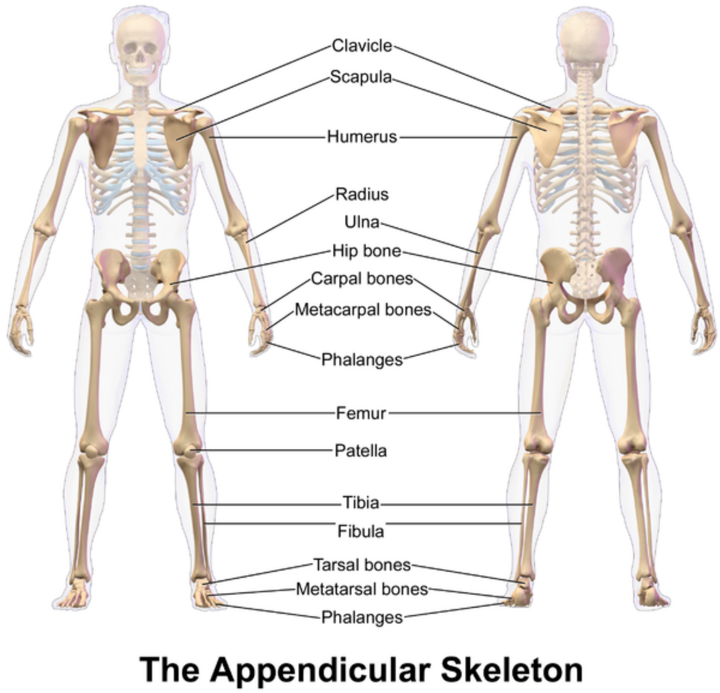

***Figure* 2.2.4** - *Appendicular Skeleton*

Function of Bone

Bones function to:

1. give structural support to the body
2. protect vital organs
3. provide an environment for the production of red blood cells
4. store minerals like calcium
5. aid in movement of the body

Bone Types

There are four types of bones based on shape.

1. Long bones: long central shaft (diaphysis) and two knobby ends (epiphysis); e.g., femur
2. Short bones: about as long as wide; e.g., patella
3. Flat bones: characterized by being relatively thin and flat, e.g., sternum
4. Irregular bones: odd-shaped bones; e.g., vertebrae

Bones can also be classified based on their origin and texture, but for the purposes of this class you need only be familiar with the types based on shape.

You should spend some time on the website eSkeletons in order to familiarize yourself with the look of the various bones listed above in the different primates.

Types of Bone Cells

1. Osteoblast: forms new bone tissue
2. Osteoclast: absorbs and removes unwanted tissue
3. Osteocyte: maintains bone as living tissue
4. Hematopoietic: produces red blood cells

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Study Guide

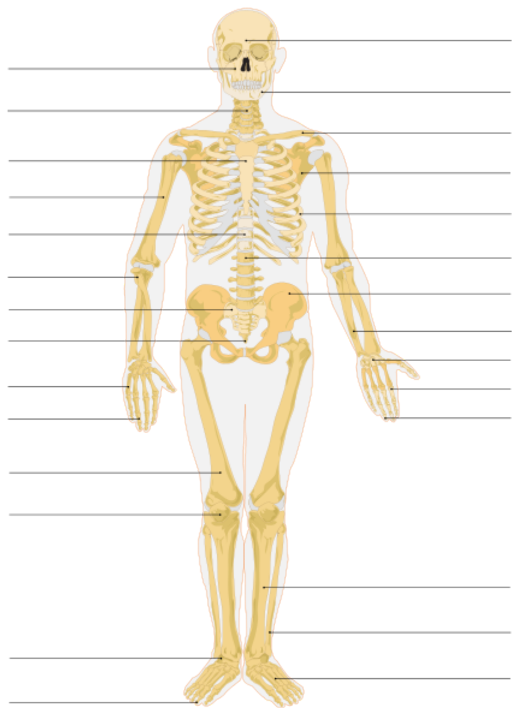

***Figure 2.2.5** - Human skeleton diagram*

Print this blank image to make your own study guide of the human skeleton

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2.3: Modern Primates

Anthropology is the study of humans and the human condition. Humans are primates. We belong to the taxonomic order Primates (pronounced *pry may tees*). This order encompasses humans as well as what we call non-human primates. Non-human primates are our closest biological and evolutionary relatives. So, we study them in anthropology in order to learn more about ourselves.

***Figure* 2.3.1** *: Golden Lion Tamarin. Woodland Park Zoo, Seattle, WA 9/30/2011*

General Mammalian Characteristics

The earliest evidence of mammals is from the Mesozoic era, however, there is limited fossil evidence and the fossils that have been found are mouse-like forms with quadrupedal locomotion. Primates evolved from an ancestral mammal during the Cenozoic era and share many characteristics with other mammals. The Cenozoic is the era of the adaptive radiation of mammals with thirty different mammalian orders evolving.

Some of the general characteristics of mammals includes:

- mammary glands: females produce milk to feed young during their immediate post-natal growth period
- hair: mammals have hair (sometimes called fur) that covers all or parts of their body
- jaw: the lower jaw is a single bone
- ear: the middle ear contains three bones: stapes (stirrup), incus (anvil), and malleus (hammer)
- heart: four-chambered heart
- aortic artery: main artery leaving the heart curves to the left to form the aortic arch
- diaphragm: mammals have one
- endothermy: mammals regulate their body temperature to maintain homeostais (a constant body temperature)
- diphyodonty: teeth are replaced only once during lifetime

General primate characteristics

While primates share traits with other mammals, such as mammary glands and endothermy, there are a number of derived traits that all primates share. Because humans share an evolutionary history with non-human primates (we share an ancestral primate), we share certain biological and behavioral traits with them.

Body

Primates have a **flexible** and **generalized** limb structure that's able to move readily in many directions. Compare the flexibility of the spider monkeys on the left with the horse on the right.

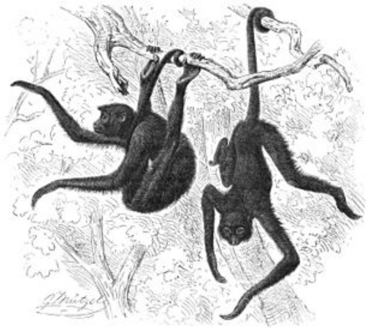

Figure 2.3.2: Spider monkeys

Figure 2.3.3: Horse

Hands

Primates have **prehensile** hands (and most of them have prehensile feet also). This means that they have the ability to grasp and manipulate objects. Primates have 5 digits (**pentadactyly**) on their hands and feet. Note that a few primates, like spider monkeys, have what are called **vestigial** thumbs. This means that they have either a very small or non-existent external thumb (but in that case, they will still have a small internal thumb bone).

Figure 2.3.4: Primate hands and feet

Primates have flattened nails instead of claws. Primates also have very sensitive tactile pads on their digits with fingerprints (**dermatoglyphs**). Some monkeys, like woolly monkeys, have similar pads with fingerprints on the ends of their prehensile tails. Therefore, it functions just like another hand. Check out the similarities and differences of the various primate hands in Figure 2.3.4.

Teeth

Primates have **heterodonty**, meaning that they have different teeth that perform different tasks when processing food via biting or chewing. With this, they have an ability to have a more **generalized** diet (compared to a specialist diet), meaning that they have more dietary flexibility. Why would this be a good thing to have?

Compare the teeth of the cayman (a relative of crocodiles and alligators) with the human teeth on the right. While the cayman's teeth do vary in size, they don't vary in structure. However, the human has incisors, canines, premolars, and molars -- all of which perform different food processing tasks.

***Figure* $2.3.5$**: *Cayman*

***Figure* $2.3.6$**: *Human jawbone*

Senses

Compared to most other mammals, primates have an increased reliance on **vision** and a decreased reliance on their senses of smell and hearing. Associated with this are their smaller, flattened noses, loss of whiskers, and relatively small, hairless ears. Also associated with this are their forward facing eyes with accompanying **binocular or stereoscopic vision**. This type of vision means that both eyes have nearly the same field of vision with a lot of overlap between them. It provides wonderful depth perception (but a loss of peripheral vision).

Note first how the eyes of the monkey on the left are more front-facing than the eyes of the cow on the right. Also note how flat the monkey's nose is and how small its ears are, when compared to those of the cow.

***Figure* $2.3.7$**: *Monkey*

***Figure* $2.3.8$**: *Cow*

Brain

In relation to other mammals, primates have a more expanded and elaborate brain. Compare the complexity of the human brain on the left to the cat brain on the right.

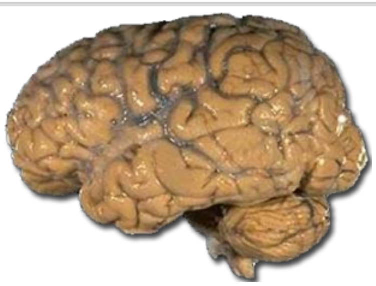

***Figure* $2.3.9$**: *Human brain*

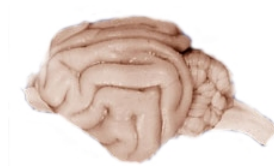

***Figure* $2.3.10$**: *Cat brain*

Life history

Life history refers to the pattern that an organism takes from conception to death. When compared to other mammals, primates have:

- longer gestation (pregnancy) periods

- reduced number of offspring (usually one, but some species commonly have twins)
- delayed maturation, with a long infancy and juvenile learning period
- extension of the entire lifespan

***Figure* $2.3.11$** *: Chimpanzee mother and baby*

Behavior

The behavioral traits we share with other primates include:

- a greater dependence on flexible, learned behavior
- a tendency to live in social groups

Figure* $2.3.12$*: *Baboons crossing the road*

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2.4: Taxonomy of the Living Primates

There are over 200 species and 600+ subspecies of primates living today. They vary in size from the tiny mouse lemur, weighing in at a whopping two ounces to the male silverback gorilla who can weigh up to 400 pounds. Some are vegetarian while others are omnivores. Many live in tropical areas, but there is at least one species that lives in a temperate region where it snows. Some live exclusively in trees and others live exclusively on the ground. The diversity of primates is expressed in the classification system.

Two Systems of Classification

The ***traditional classification*** approach put the primates into two suborders: Prosimii and Anthropoidea. The Prosimii contained lemurs, lorises, and tarsiers while anthropoidea consisted of monkeys and apes. The traditional classification approach used levels of taxonomic complexity to determine which suborder a primate should belong.

Most primatologists today use an approach that uses ancestral-descendent relationships to determine the suborder. In this biochemical ***evolutionary classification*** approach, there are also two suborders, but they are called **Strepsirhini**, which includes lemurs, aye ayes, galagos, and lorises, and **Haplorhini**, which includes tarsiers, monkeys, apes, and humans.

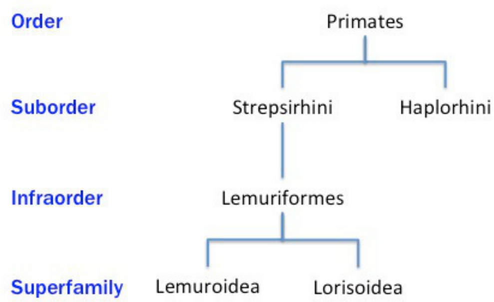

***Figure* $2.4.2$** - *Strepsirhini classification*

Strepsirhini, which means "twist-nose," characteristics include:

- snout-like nose
- wet rhinarium (naked, moist area of skin on the snout--think dog nose)
- heightened sense of smell
- prominent whiskers
- divided upper lip tied to the gums by a membrane
- wooly fur
- grooming claw
- dental combs (tooth comb)

Most Strepsirhines are nocturnal and arboreal and have specialized features, such as large eyes with a light reflecting disk, to help with night vision. They were the first suborder of primates to evolve (O'Neil 1998-2012) and are sometimes referred to as the "lower primates."

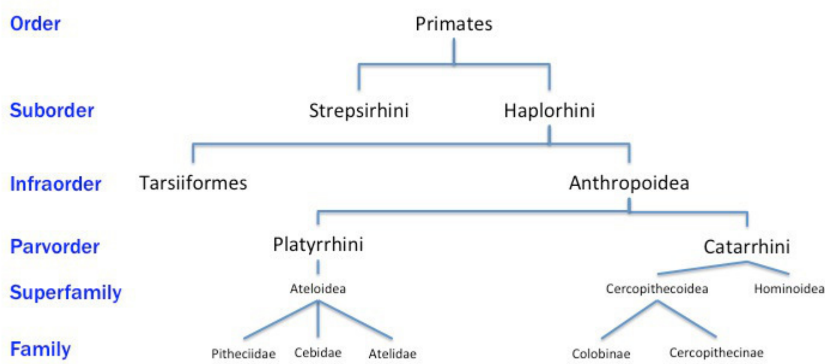

***Figure* $2.4.3$** - *Abbreviated Haplorhini classification*

Haplorhini, which means "simple nose," characteristics include:

- relatively flattened faces (when compared to Strepsirhini)
- forward facing eyes
- postorbital enclosure (bony plate encloses back of eye socket)
- dry noses
- decreased reliance on sense of smell
- larger brains and body size (when compared to Strepsirhini)
- diastema (space between upper lateral incisor and upper canine tooth) except in humans
- increased gestation, maturation, and parental care
- more mutual grooming

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2.5: Primate Ecology

Primate ecology is the study of the relationship between primates and their environment. Their environment includes not only the physical environment (e.g., trees, water, weather) but also the other animals in the environment, including other non-human primates and even humans. Why should we care about primates and their ecology? Remember that evolution is always environmentally dependent, so the environment is the main thing that we have to consider when examining a primate, its biology, and behavior. Also, keep in mind that primates are not only affected by their environments, they affect their environments as well (by eating plants and insects, dispersing seeds, etc.).

***Figure* 2.5.1** - *Monkey feeding*

There are two primary environmental factors that primate ecologists focus on: Food and Predators.

1) **Food**

- **Primatologists** (scientists who study primates) examine the quality, quantity, and distribution of food in a primate's environment.
- Why? Because food = babies. This means that those individuals who acquire more high-quality food more efficiently are likely to have more offspring and therefore will be more evolutionarily successful.
- This pressure is greater for females than for males, because of the biological costs associated with reproduction (**reproductive asymmetry**). Remember that primates spend a very long time as dependent nursing infants, so primate mothers have a heavy burden when caring for them (the only exceptions are some New World monkeys: the father cares for the infants, but the mother still nurses them).

2) **Predators**

- Primatologists also examine the types and distribution of potential predators in a primate's ecosystem.
- Why? Because no one wants to get eaten, right? Those who can most efficiently and effectively avoid predation are likely to have more offspring and therefore will be more evolutionarily successful.

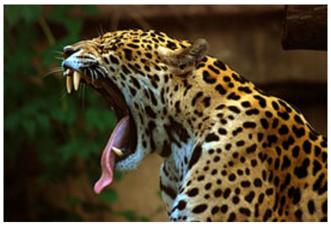

***Figure* 2.5.2** - *Jaguar*

Primatologists also look at other environmental factors, such as:

- weather
- the distribution of water
- the distribution of sleeping sites, and
- the primate's relationships with other individuals within their social group, other groups of their own species, and other species (including humans).

Food

***Figure* 2.5.3** - *Baboon examining a leaf*

Most primates are **herbivores** (they eat plant foods) and are fairly generalist in their dietary habits. Some primates are **omnivores** and eat lots of things (plant and animal). However, some primates are more specialized.

- **Folivores**: eat mainly leaves.
- **Frugivores**: eat mainly fruit.
- **Insectivores**: eat mainly insects.
- **Gummivores**: eat mainly tree sap.

***Figure* 2.5.4** - *Lemur eating fruit*

One of the challenges that primates face in their day-to-day life is a type of **evolutionary arms race** they have with their food. Some food items, like fruit, "want" to be eaten. In other words, it's evolutionarily advantageous for a fruit to be eaten by a primate, who then carries the fruit's seeds far away from the parent plant in its stomach, to deposit them elsewhere. The fruit benefits from this **seed dispersal**, thereby limiting competition between the parent plant and its offspring. This is one of the hypothesized reasons that fruits have high sugar or fat contents, to make them attractive to seed dispersers, such as primates and birds.

However, some food items, like leaves, don't "want" to be eaten. It's not evolutionarily advantageous for a plant to be stripped of its leaves. A leafless tree would not be able to perform photosynthesis and would promptly die. This is why plants have developed certain chemicals, called **secondary compounds** or **antifeedants**, in their leaves. These chemicals make the leaves unpalatable or indigestible to primates. In these cases, scientists have determined that primates have developed behavioral methods to avoid consuming antifeedants. For example, most leaf-eating monkeys prefer to eat young leaves, which are visually identifiable (either lighter in color or a different color) and higher in nutrients and lower in indigestible fiber and antifeedants, than mature leaves.

Not only have primates developed behavioral strategies to meet these challenges, some primates have evolved different types of color vision in order to forage for food and other primates have developed specialized digestive systems to deal with low-quality (high-fiber, high-antifeedant) foods.

***Figure* 2.5.5** - *Black and white colobus monkey resting*

Activity budgets

How a primate spends its time is called its **activity budget**. These are comprised of the major categories of:

- foraging/feeding
- social behavior
- locomotion/traveling, and
- resting/sleeping

Why should we care about activity budgets?

Examining a primate's activity budget gives primatologists a good idea of how that particular primate (or primate group) "makes a living". For example, if squirrel monkey (pictured right) Group A spends 30% of its time foraging and squirrel monkey Group B spends 40% of its time foraging, then one can assume that there is something going on that is causing the difference. One can form possible hypotheses such as: Group B is larger than Group A and has more mouths to feed and therefore has to spend more time looking for food to feed them OR Group B has less food in its area than does Group A and so has to spend more time searching for it.

Remember also that if a primate has to spend more time eating or moving around in order to find something to eat, then they are having to spend less time either resting or socializing. Primates only have a finite amount of time in their day, so they have to maximize the use of it the best they can within their environmental parameters.

Activity budgets denote **when** a primate is "making a living":

- **Diurnal**: active during the day. Most primates are diurnal.
- **Nocturnal**: active during the night.
- **Crepuscular**: active during dawn and dusk. Ring-tailed lemurs (pictured below left) have this activity pattern.
- **Cathemeral**: active during irregular periods during day and night. Black lemurs (pictured below right) are one of the few primate species who have this activity pattern.

***Figure* $2.5.6$** *- Ringtailed lemur*

***Figure* $2.5.7$** *- Black lemurs*

Note that these activity patterns are not hard and fast rules. As with diet, there is a lot of variation in how flexible a particular species (or group within a species) is when it comes to their activity patterns. For example, although traditionally thought of as strictly nocturnal, the activity patterns of owl monkeys have been found to be highly sensitive to environmental factors such as temperature and amount of moonlight.

Food and Feeding Competition

One of the main factors that affects a primate "making a living" is **feeding competition** (competing with others for food).

There are two groups that a primate competes with;

- the other primates in its social group (AKA **within-group competition**)
- primates (of the same species) in other groups (AKA **between-group competition**)

***Figure 2.5.8** - Macaques fighting*

There are also two types of competition. The type of competition prevalent in a situation depends on the quality and quantity of food available in the environment.

- **Scramble competition**: happens when there is a lot of low quality food. This is more common for leaf-eating primates, because trees tend to have large quantities of edible leaves (although some types, such as young leaves, may be preferable to others). It's an indirect competition in which whoever finds food faster or eats faster gets more food than do other individuals.
- **Contest competition**: happens when there is a small amount of high quality food. This is more common for fruit-eating primates, because a fruiting tree has a limited amount of high-quality fruit. It's a direct competition, where certain individuals (stronger, higher social status) get more food than do other individuals via squabbling or fighting.

In total, one can have:

- within-group scramble competition
- within-group contest competition
- between-group scramble competition, and
- between-group contest competition.

Feeding competition can be severe and have serious effects on the health, well-being, and reproductive capacities of primates. In other words, it has a direct effect on their evolutionary fitness. As expected, primates demonstrate a lot of behavioral strategies to deal with the feeding competition they face. For example, a group with high scramble competition may spread out more when feeding so as to access more resources OR in a group with high contest competition, some individuals may form coalitions in order to "gang up on" other primates to take their food.

Spatial use: home ranges and territories

The area that a primate uses is its **home range**. The part of the home range that's used most often is the **core area**. Some species, such as snub-nosed monkeys, have very large home ranges (32 sq. km) and other species, such as the pygmy marmoset, have very small ones (0.003 sq. km). A primate's home range has to contain all of the resources it needs in order to survive (food, water, sleeping sites, etc.). The home ranges of different primate groups often overlap, sometimes only a little, but sometimes a lot. If the home range is physically defended, it's a **territory**. Chimpanzees are famous for their territorial conflicts, which are so organized and violent that scientists have begun calling it "warfare".

Primate Behavior

As noted in a previous section (The Modern Non-Human Primates), one of the fundamental traits that primates share is that we are **social** creatures. All primates share some form of social structure with others of their own species, whether that be in a large permanent social group or as an individual who has repeated short-term interactions with others. The social relationships that primates have with other members of their own species have a huge impact on the individuals involved and are incredibly important to their health, well-being, and reproductive success. Therefore, the study of primate social behavior has been a focus of primatologists for the last 50 years.

Primate behavior studies come in three formats:

Figure 2.5.9 - Chimpanzees in captivity

- **Captive**: The animals are in captivity. Variables are easy to control in these situations (for example, the number of individuals in a group or food availability) and the primates are easier to observe at close-range. However, because of the artificiality of the situation, the primates may not be exhibiting normal behavior.
- **Semi-captive (AKA semi-free-ranging)**: The animals are captive, but in a very large area like an island or a fenced-in compound. Variables are still relatively easy to control and the primates are easier to observe (than in the wild). The primates tend to exhibit more natural behavior patterns in this type of setting than when compared to a completely captive situation.
- **Free-ranging**: The animals are living in the wild, in their natural environment. This is the most logistically difficult type of primate study. The animals are more difficult to observe (often requiring a **habituation** period to get them accustomed to the presence of observers). However, the primates are most likely to perform their normal array of behaviors in this type of study.

Social structure: the "whys" and the "hows"

The basic premise of why primates have certain social behaviors is due to **reproductive asymmetry**. Remember (from "Food", on this page) that females are under a lot more pressure than males to forage effectively because of the biological pressures they're under (due to the burden of reproduction). It is precisely this inequality that causes the sexes to have different evolutionary priorities:

- For **females**, their priority is **food**. Females can only reproduce at a certain rate, due to the length of time it takes to be pregnant, raise an infant to independence, and have their bodies recover to do it all over again. Access to lots of good quality food through little effort is the key to accomplishing this task.
- For **males**, their priority is finding **mates**. Males can reproduce at a much faster rate than can females. The only real constraint on their reproductive rate is how frequently they can get fertile females to mate with them.

So, **primate social structure** works like this:

- male distribution follows how the females distribute themselves, and
- the females distribute themselves depending on how the food is laid out in their environment.

Social groups have two **immigration/emigration** patterns:

Figure 2.5.10 - Baboon social group

Female philopatry:

- Females do not emigrate from their birth group at sexual maturity.
- Males usually emigrate from their birth group at sexual maturity.
- Females form the core of the group, are biologically related, and have tight social bonds (often exhibited through social cooperation and grooming: seen in these baboons, pictured right). Males do not have much in the way of positive social relationships .
- This is the most common form of social system in primates.

Male philopatry:

- Males do not emigrate from their birth group at sexual maturity.
- Females usually emigrate from their birth group at sexual maturity.
- Males form the core of the group, are related. and have tight social bonds. Females do not have much in the way of positive social relationships.
- This type of social system tends to happen when resources are widely dispersed, so females are widespread and difficult for the males to consistently access (as in the spider monkey, pictured right).

Social strategies

Figure $2.5.11$

In order to achieve their priorities, male and females must utilize certain social strategies to gain success.

Dominance

- As with chickens, primates have a "pecking order" or **dominance hierarchy** in their social groups.
- One's position in the dominance hierachy often gives them access to preferred resources, including not only food and mates, but other resources such as sleeping sites and water.
- Sometimes dominance hierarchies are determined through fighting, but more often they are sorted out through a series of aggressive/submissive non-contact interactions, such as approach/avoidance, facial expressions, and body postures. Primates try to avoid direct aggressive contact in an effort to avoid risk of bodily harm.

Figure $2.5.12$ - *Macaques grooming*

Cooperation

- Dominance hierarchies aren't completely linear. One's rank in the hierarchy often depends on who they can get to cooperate with them during conflicts. For example, Monkey 2 may be submissive to Monkey 1 when alone, but when her buddy Monkey 3 is around, the two of them cooperate and chase Monkey 1 away from food together. Therefore, Monkey 2's position in the dominance hierarchy is situationally dependent.
- These cooperative relationships are usually between relatives. In male philopatric groups, they're usually brothers. In female philopatric groups, it's often mother-offspring or siblings.
- The relationships are cultivated through **affiliative** behaviors, such as play, grooming, and other forms of body contact (e.g., hugging). So, primates practice *You scratch my back, I'll scratch yours* both literally and figuratively.

VIDEO: How bonobos use play as a tool

Why be in a social group?

***Figure* 2.5.13**

So, why would a primate choose to be in a social group if it is just one big mess of food competition, mate competition, and political posturing? Well, because there are benefits, of course!

Living in a social group:

- provides access to **mates**. While there is, of course, competition for mates within the group, a social group ensures that there are at least mates available to fight over.
- provides more eyes looking for **food** and more brains remembering where food is in the ecosystem
- provides **anti-predator defense**

- There are more eyes on the lookout for predators.

- An additional anti-predator benefit is known as "The Selfish Herd" (AKA safety in numbers). It basically comes down to "you don't have to run faster than the predator, just faster than the other guy".

- Some social groups will "mob" predators and drive them away. This only works on smaller predators, especially those who rely on surprise attacks (such as the Harpy Eagle, pictured right).

Types of primate social groups

Solitary:

***Figure* 2.5.14** - *Galago*

- Males are alone most of the time, except when seeking out mates. Females live with their dependent offspring.
- One male will have territorial overlap with several females.
- Some prosimians have this social system (like the galago, pictured right).

Monogamy:

***Figure* 2.5.15** - *Titi monkey*

- A social group is comprised of a male, a female, and their dependent offspring.
- This is also called "pair bonded".
- This is common in New World monkeys (for example, titi monkeys, pictured right) and the "lesser apes" (siamangs and gibbons).

Single-male multifemale:

***Figure* $2.5.16$** *- Diana monkey*

- A social group is comprised of one adult male, several (to many) adult females, and their dependent offspring.
- Males that don't belong to a social group may either live alone or in multimale (bachelor) groups that have no females.
- It's a difficult life for the resident male in these social groups, because not only did he have to fight his way into the group (either driving the previous resident male out or stealing females from another male), he has to continually fight to keep other males out of his group, while keeping the females in the group.
- When males take over groups, some may commit infanticide (killing the previous resident male's infants).
- This is a common social group in Old World monkeys (like the Diana monkey, pictured right)

Multimale-multifemale

***Figure* $2.5.17$** *- Hanuman langur*

- A social group is comprised of more than one adult male, more than one adult female, and their dependent offspring
- In these groups, in order to have preferential access to females, males will form dominance hierarchies or develop biological characteristics that the females find attractive. For example, during the mating season, squirrel monkey males begin storing large amounts of water and fat on their bodies.
- Some species (such as Hanuman langurs - pictured right) have both single-male and multimale multifemale social groups in the same population.

Fission-fusion

***Figure* $2.5.18$** *- Bonobo*

- In this situation, individuals belong to a large group called a community. Each community has a home range and consistent community membership. Within the community, individuals form temporary foraging groups called parties. Parties have an unpredictable membership. So, on any given day (or even part of a day), one cannot predict who will be foraging with whom.
- Females always travel with their dependent offspring.
- Sometimes males form partnerships and forage together.

- This type of social group is thought to have been an adaptation to environments with patchy, unpredictable fruit availability.
- It's found in chimpanzees, bonobos (pictured right), and spider monkeys.

Single-female multimale

Figure $\mathbf{2.5.19}$ - *Tamarins*

- A social group is comprised of one adult female, more than one adult male, and their dependent offspring.
- This is rare in primates.
- Found in marmosets and tamarins (pictured right), this type of social system is thought to be an adaptation to the twinning (giving birth to twins) that it common to these small primates. The males carry the dependent infants.

2.6: Overviews of Living Primates (Strepsirhines)

***Figure* 2.6.1** - *White-headed Lemur, Masoala National Park, Madagascar*

The following pages provide a very brief overview of some of the primates living today. It is not in any way a complete list of the hundreds of primate species. It is intended to give you a basic idea of the behaviors of some of the Strepsirhines and Haplorhines. If you would like to learn more about the primates mentioned on the overview pages, check out the reference section, which has links to sources with more details.

The Strepsirhines

Lemuroidea

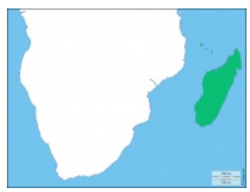

***Figure* 2.6.2** - *Distribution of lemurs (modified from original map from http://d-maps.com/carte.php?num_car=742&lang=en)*

***Figure* 2.6.3** - Varecia variegata *foot with toilet-claw*

Lemurs, which means "ghosts," are small primitive primates ranging in size from about two ounces for the lesser mouse lemur to about 13 pounds for the Indri. They have a wet rhinarium, which indicates that the sense of smell is important. They have a dental comb and a "toilet claw" (grooming claw located on the second toe of the hind foot) both of which are used for grooming; the toilet claw is also used while eating. With the exception of the mouse lemur, lemurs are hindlimb-dominated quadrupedalists who are found equally in trees and on the ground. Many of the species, including sportive and ring-tailed lemurs, scent mark their territories.

There are two superfamilies of Strepsirhines: 1) Lemuroidea, which includes the families Cheirogaleidae, Daubentoniidae, Indriidae, Lemuridae, and Leipilemuridae, and 2) Lorisidea, which include the families Lorisidae and Galagidae.

Mouse and Dwarf Lemurs

***Figure* 2.6.4** - *Gray mouse lemur (Microcebus murinus)*

Cheirogaleidae, or mouse and dwarf lemurs, are nocturnal, arboreal insectivores that move around by hopping on their hind legs and leaping. They live in the forests of Madagascar. There are five genera: 1) *Cheirogaleus*, e.g., fat-tailed dwarf lemur and furry-eared dwarf lemur, 2) *Microcebus*, e.g., golden-brown mouse lemur and pygmy mouse lemur, 3) *Mirza*, i.e., Coquerel's giant mouse lemur and northern giant mouse lemur, 4) *Allocebus*, i.e., hairy-eared dwarf lemur, and 5) *Phaner*, e.g., pale fork-eared lemur and Amber Mountain fork-eared lemur, and twenty-one species. Cheirogaleus , Phaner , and Mirza live in monogamous family groups while Microcebus lives in multi-male, multi-female groups. Females bear two to three offspring at a time. Gestation periods vary from 60 days for the smallest species to 89 days for the larger species. Females have three nipples, which is a trait not shared by any of the other lemurs. Mouse lemurs' tails are at least as long as their bodies. There is some variety in diet although most dwarf and mouse lemurs are omnivorous, but some species specialize, such as Phaner that eats primarily gums.

True Lemurs

***Figure* 2.6.5** - *Eulemur mongoz*

Lemuridae, or true lemurs, are diurnal primates about the size of the typical domestic cat. They have long, heavily furred tails, tufts of fur at the tips of their ears, and a long snout. Their eyes are smaller in comparison to other Strepsirhines. Found on Madagascar and the Comoro Islands, true lemurs spend a lot of time of the ground, but general rest and sleep in trees. They are vertical climbers and leapers who eat leaves, fruits, and some insects. Several of the true lemur species live in large multi-male, multi-female groups where the females dominate the males. Females also tend to defend the group even though males are generally larger than females (in other words true lemurs exhibit sexual dimorphism). Other true lemurs are solitary. There are twenty-three species of true lemurs and five extant genera: 1) *Lemur*, i.e, ring-tailed lemur, 2) *Eulemur*, e.g., brown lemurs and mongoose lemurs, 3) *Varecia*, e.g., red ruffed lemur, 4) *Hapalemur*, e.g., golden bamboo lemur, and 5) *Prolemur*, i.e., greater bamboo lemur.

Sportive lemurs

***Figure* $2.6.6$** - *Red-tailed Sportive Lemur, Kirindy, Madagascar.*

“The sportive lemur (*Lepilemur spp.*) received its name because, when threatened, it turns and raises its arms as if preparing to box” (Blashfield 2004: 2548). There are several species of sportive lemurs, including the red-tailed sportive lemur, the white-footed sportive lemur, and the northern sportive lemur. They live in the dry, evergreen forests of Madagascar. Sportive lemurs are also called weasel lemurs and weigh from 1.1 to 2.2 lbs. They have short, pointed head and large round ears. They also only have 32 teeth as compared to the true lemurs that have 36 teeth. Sportive lemurs are primarily folivores, but also eat bark, flowers, and fruit. Sportive lemurs are the only lemurs to exhibit cecotrophy [SEE cuh troh fee]. This means that they eat their own waste material that contains partially plant material in order to get as much nutrition as possible. Sportive lemurs are nocturnal vertical climbers and leapers. Males usually live alone and defend their territory from others using vocalizations, chasing, and, if necessary, fighting. Males can mate with multiple females during the mating season. Females bear one young after a gestation period of about four and a half months. Infants stay with the mother for about one year.

Leaping Lemurs

***Figure* $2.6.7$** - *Indri female and infant.*

Indriids or leaping lemurs include sifakas (*Propithecus*), Indiri (*Indri*), and wooly lemurs (*Avahi*). They live in the rainforests, deciduous forests, and evergreen forests of Madagascar. The Indri is the largest of not only the Indriids, but the Strepsirhini in general. There is some variation in the appearance of the various Indriids. Sifakas do not have fur on their face and have sparse hair on their underside. Indris have silky fur and a stumpy tail and woolly lemurs have thick, woolly fur (as indicated by their name) and ears that are barely visible in their fur. One of the characteristics that unite the Indriids is the presence of 30 teeth instead of 36 like true lemurs. With the exception of the avahis, Indriids are diurnal. All of them are vertical climbers and leapers, leaping from tree to tree and leaping when on the ground (watch this short video to see some sifakas in (loco)motion: youtu.be/8RiZElNNpAY). In fact, Indris can leap up to 10 ft in a single bound. They live in small groups, which may be multi-male, multi-female or solitary/all male. Males, which are dominant, are responsible for defense of territories and indirectly contribute to infant care. Females bear one offspring at a time after a gestation period of 130-150 days. Indriids are vegetarian, focusing on leaves, buds, fruits, flowers, and bark.

Aye-aye

***Figure* 2.6.8** - *Aye-aye.*

Named after the sound it makes, the aye-aye has only 18 teeth; its incisors grow continually, and it lacks a toilet claw. It has large eyes, making them optimal for its nocturnal lifeway. Aye-ayes average about 3 ft in length. It has large, pointed ears and a pointed nose and chin. There is an extra-long middle finger with a hooked claw that is used when hunting for insects, to probe and scrape for insect larvae, and to clean its fur (watch this video from the Duke Lemur Center to see the aye-aye in action: youtu.be/HB_fQ1Rg_K4). While aye-ayes are classified as insectivores, they also eat parts of Ramy and palm nuts, fungi, and fruit. These solitary quadrupeds breed throughout the year. Gestation is about 170 days and females usually have one infant at a time, normally with over a year between births. Female ranges do not overlap, but male ranges may, which occasionally results in conflict between the two males.

Lorisoidea

***Figure* 2.6.9** - *Distribution of lorises, pottos, and galagos. Original blank map from http://d-maps.com/carte.php?num_car=3266&lang=en modified from world map to show range of lorises.*

***Figure* 2.6.10** - *Sri Lankan Slender Loris.*

Lorises and Pottos

There are five genera (*Arctocebus*, *Perodicticus*, *Pseudopotto*, *Loris*, and *Nycticebus*) and about fifteen species of Lorisidae (pottos and lorises) living in sub-Saharan Africa, southeast Asia, southwest China, southern India, and Sir Lanka. These small primates weigh in from nine ounces to two pounds. To survive in areas where monkeys live, these lorisids are nocturnal so that they do not have to compete directly with monkeys. Like other nocturnal Strepsirhines, they have a reflective layer at the back of their larger eyes to help them see in the dark. Also like many of the other Strepsirhines, lorisids have a wet rhinarium, albeit short, and dental comb. All of their digits have claws, but the one on the second toe is longer, thereby qualifying as a toilet claw. They have an opposable first toe that allows them to grasp branches securely; in fact, lorisids can be found feeding while hanging upside down from tree branches! These arboreal primates prefer to forage for food on their own. While each species may have a food preference, in general lorisids are omnivores and eat insects, fruit, gum, small vertebrates, and birds' eggs. Many lorisids exhibit a form of quadrupedal locomotion called cryptic locomotion, which means that they move slowly and deliberately. This form of locomotion helps to keep them hidden from predators; they can stay still for hours at a time. In an unusual Strepsirhine predator-avoidance adaptation, Perodicticus potto has three or four skin-covered bony spines behind its neck. This potto will tuck its head and turn the spines toward attackers in an effort to ward off a predator. After one of the longest gestation periods, 193 days, females usually give birth to two offspring who are fully matured after ten to eighteen months.

***Figure* 2.6.11** - *Galago granti*

Galagos

Galagos used to be classified as a subfamily of Lorisidae, but are now classified as a separate family, Galagidae. Generally referred to as bushbabies because their cry sounds like a mewling infant, galagos are small vertical climbers and leapers who can jump up to 15 feet, using their busy tails as balance. Their arms are longer than most primates in proportion to other primates. They have soft pads on the tips of their fingers that help them cling to branches. They can move quickly, snatching flying insects in midair, which they stir up using vocalizations. Galago ears "are so important that they can fold, like an accordion, when the little animal is moving quickly through prickly or otherwise dangerous leaves" (Blashfield 2014: 2608). After a night of hunting, galagos will sleep together in a communal sleeping hole in a tree. Like pottos and lorises, galago females usually give birth to two offspring who she carries around in her mouth for about two weeks after birth. A female galago and her offspring defend a territory from foreign females. Males also defend a territory that encompasses several female territories.

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2.7: Overviews of Living Primates (Haplorhines)

As you no doubt recall, Haplorhini means "simple nose." The shared characteristics of tarsiers, New World monkeys, Old World monkeys, and apes include:

- relatively flattened faces (when compared to Strepsirhini)
- forward facing eyes
- postorbital enclosure (bony plate encloses back of eye socket)
- dry noses
- decreased reliance on sense of smell
- larger brains and body size (when compared to Strepsirhini)
- diastema (space between upper lateral incisor and upper canine tooth) except in humans
- increased gestation, maturation, and parental care
- more mutual grooming

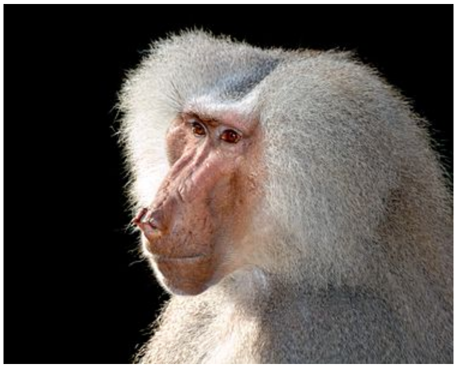

Figure* $2.7.1$*: Hamadryas Baboon *(Papio hamadryas)* at the Leipzig Zoo.

Tarsiers

The three genera of Tarsiidae;

1. *Carlito*,
2. *Cephalopachus*, and
3. *Tarsius*,

Eighteen species living among the islands of southeast Asia, including Borneo, Sumatra, and some of the Philippines. Tarsiers are arboreal vertical climbers and leapers and can be (not so easily) found in dense rainforest. They are occasionally found in non-forested habitats only if there are enough vertical surfaces for leaping and clinging. They rarely spend time on the ground. Tarsiers are sometimes called "living fossils" because of their close resemblance to fossil primates dated to about 40 million years ago. They are small primates, weighing about 4 ounces and roughly 5 inches in length, although with their tail, which may have a tuft of fur on the end, they almost double in length. Like some Strepsirhines, tarsiers have toilet claws and 36 teeth. They are also nocturnal or crepuscular and have huge eyes (just one of their eyes weighs as much as its brain!). In fact, under the traditional classification scheme, tarsiers were classified as prosimians; however, in the new classification system, tarsiers are Haplorhines because they do not have a wet rhinarium. Tarsiers can turn their heads 180 degrees and have the longest hind limb to forelimb proportion of any mammal. Because tarsiers are difficult to locate in the wild, it appears that reproduction is seasonal. Females give birth to a single offspring who weigh from 25 to 30% of the mother's body weight. When infants are born they can immediately cling and climb. The mother is the primary caretaker, although dominant males and subadult females may help. Most tarsiers spend their waking hours alone hunting (they are the only true carnivorous primate), but sleep in small groups during the day. Tarsiers are territorial with male and females ranges overlapping.

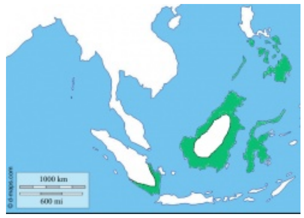

Figure 2.7.2 *- Distribution of tarsiers. Original map from http://d-maps.com/pays.php?num_pay=67&lang=en modified to show distribution of tarsiers.*

Figure 2.7.3 - Tarsier *(Carlito syrichta)*, Bohol, Philippines.

New World Monkeys

There are several families of New World Monkeys (NWMs):

1. Callitrichidae (i.e., marmosets and tamarins)
2. Cebidae (i.e., squirrel monkeys and capuchins)
3. Aotidae (i.e., night monkeys)
4. Pitheciidae (e.g., sakis and titis) and
5. Atelidae (i.e., howler monkeys and spider monkeys).

The 70+ species are found in Central and South America. All NWMs are arboreal although some will spend a little time on the ground. All are diurnal with the exception of the night monkey, which is nocturnal. All are quadrupeds, except for the spider monkey, which is a semi-brachiator. Some have prehensile tails, or "grasping" tails that serve as a fifth limb. Most, but not all, live in multi-male, multi-female groups. NWMs have flat noses with nostrils that are set far apart, wide open, and facing outwards.

Figure 2.7.4 *- Distribution of New World Monkeys. Original blank map from http://d-maps.com/pays.php?num_pay=299&lang=en modified to show range of New World Monkeys.*

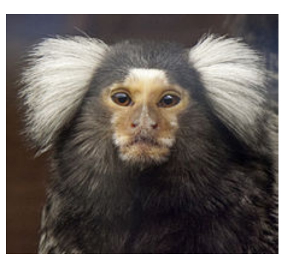

Figure 2.7.5 *- White-eared Marmoset (notice the nostrils).*

They have strong big toes that are “strongly opposable but their thumbs are imperfectly opposable and their fingers cannot grip well” (Natural History Collections…2001-2007). NWMs have twelve premolars unlike their counterparts in the Old World who have eight premolars. The territories of different groups within various NWM species frequently overlap and sometimes “friendships” develop between the different species (Blashfield 2014).

New World Monkeys: Callitrichidae

Callitrichids are small primates, including the smallest monkey, the pygmy marmoset, which weighs about 3.5 ounces when fully mature and averages between 5-6 inches in length, who live in Central and South America. They generally have little fur on their faces, but have tufts of fur on their heads. Some of the most colorful primates belong to the Callitrichids, e.g., golden lion tamarins (pictured above). Their tails are non-prehensile and are used for balance when moving quadrupedally through the trees. Unlike most other monkeys, they have claws instead of nails except on the big toe (also called a hallux), which does have a nail, allowing them to dig into the bark of trees. Callitrichids do not have a third molar and are primarily insectivorous, but eat gums, fruit, buds, leaves, flowers, lizards, frogs, and snails as well. They live in monogamous (e.g., golden lion tamarin) or polyandrous (e.g., saddle-back tamarin) family groups. Females normally give birth to twins with the exception of Goeldi’s monkey that has single births. All individuals in the group contribute to infant care. Genera of callitrichids include *Callithrix*, e.g., buffy-headed marmoset and black-tufted marmoset, *Mico*, e.g., silvery marmoset and Emilia’s marmoset, *Cebuella*, i.e., pygmy marmoset, and *Saguinus*, e.g., Emperor tamarin and cottontop tamarin, *Callibella*, i.e., dwarf marmoset, *Callimico*, i.e., Goeldi’s marmoset, *Leontopithecus*, e.g., golden lion tamarin and black lion tamarin.

***Figure* 2.7.6** - *Golden lion tamarin family*

***Figure* 2.7.7** - Common marmoset *(Callithrix jacchus)* eating a cockroach

New World Monkeys: Cebidae

There are three genera of cebids: 1) *Cebus*, e.g., Kaapori capuchin and white-headed capuchin, 2) *Sapajus*, e.g., black capuchin and tufted capuchin, and 3) *Saimiri*, e.g., bare-eared squirrel monkey and Central American squirrel monkey. They are relatively small primates, ranging in weight from around 2.5 pounds (adult male squirrel monkey) to 8.5 pounds (adult male brown capuchin). Unlike callitrichids, cebids have a prehensile tail and the third molar. They are arboreal omnivores, focusing on fruits and insects. Females give birth to one or two offspring and are responsible for the care of their young. They live in relatively large multi-male, multi-female groups with a dominant male. Cebids perform urine washing; they urinate on their hands and then rub them on their fur and feet in order to scent mark their territory. These quadrupeds can be found in Central and South America as well as Trinidad and Tobago, Caribbean islands off the coast of Venezuela.

***Figure* $2.7.8$** - *Bolivian-squirrel-monkey*

***Figure* $2.7.9$** - White-faced capuchin *(Cebus capucinus)* on Rio Frio, Costa Rica

New World Monkeys: Aotidae

Night monkeys, also called owl monkeys, are arboreal primates living in Panama and parts of South America. They are small, weighing up to just under three pounds and exhibit no sexual dimorphism. Like other nocturnal primates, night monkeys have large eyes. Their faces are rounded and marked with three dark brown or black lines—one on either side of their eyes and one in the middle of the forehead. Sometimes it appears as if night monkeys have no ears, but actually their small, rounded ears can be hidden by thick fur. Night monkeys are monogamous; mated pairs live with two or three offspring. Females usually have a single offspring, with both parents participating in infant care. Primarily frugivores, night monkeys will also eat leaves, flowers, insects, eggs, birds, spiders, and bats. Like cebids, night monkeys practice urine washing.

***Figure* $2.7.10$** - Night monkey *(Aotus zonalis)*

New World Monkeys: Pitheciidae

The long-coated pithecids live in the various rainforest habitats in South America. These arboreal quadrupeds live in small groups. Titi monkey groups are centered on a monogamous pair while the sakis and uakaris live in multi-male, multi-female groups ranging from 10 individuals up to 100. Pithecids are territorial but generally use vocalizations instead of physical confrontation to defend their territory. All pithecids are frugivores; in fact, they are specialized frugivores called granivores who focus primarily on fruit seeds. Most pithecid females give birth to a single offspring. In general, males do not participate in infant care, although male sakis may groom their young and male titi monkeys provide the majority of care for their offspring. The four genera of pithecids are 1) *Callcebus*, e.g., titi monkeys, 2) *Cacajao*, e.g., uakaris, 3) *Chiropotes*, e.g., bearded sakis, and 4) *Pithecia*, e.g., sakis.

***Figure* 2.7.11** - *White-faced saki monkey*

***Figure* 2.7.12** - *Titi Monkey*

***Figure* 2.7.13** - Uakari *(Cacajao calvus)*

New World Monkeys: Atelidae

The arboreal atelids are found in both Central and South America, although woolly monkeys are found only in the Amazon, muriquis are in Brazil's southeaster rainforest, and yellow-tailed woolly monkeys are only in the cloud forests in the Peruvian Andes. The atelids range is size from the smaller spider monkey, weighing about 13-20 pounds, to the howler monkey, weighing up to 25 pounds. Atelids have prehensile tails with a hairless, tactile pad on the underside of the tip of the tail. This sticky pad helps the atelids hold on to things, especially tree limbs as they hang from their tails to eat. They are primarily frugivores, but will eat leaves, flowers, plant gums, and insects depending on the season. Atelids live in multi-male, multi-female groups, anywhere from two individuals up to one hundred (male howler monkeys are known to have "harems" of females). Males are philopatric; females leave their birth group. Atelids have ranges, but do not defend territories. When ranges overlap, conflict can occur. Females usually give birth to one offspring in the dry season and solely responsible for care of the young. While all of the atelids use vocalizations to communicate, howler monkeys are known for their distinctive calls, or roars, that can be heard (by humans) over a mile away.

***Figure* 2.7.14** - Howler monkey (*Alouatta caraya*)

***Figure* 2.7.15** - *Geoffrey's spider monkey*

***Figure* 2.7.16** - Woolly monkey (*Lagothrix lagotricha*)

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2.8: More Haplorhines (Old World Monkeys)

Old World monkeys (OWMs) are found in sub-Saharan Africa, southern Asia, and northern Japan. They live in a wide variety of habitats, from tropical jungle to seasonal snow and savannas. Some are arboreal and others terrestrial. There is variety of group structure, but most live in diurnal multi-male, multi-female groups. The traits that unite OWMs are:

- Lack of prehensile tail
- Forelimbs are shorter than hindlimbs
- Quadrupedal
- Narrow nostrils that are close together
- Well-developed opposable thumbs and big toes
- Presence of ischial callosities in many species (hard pads on the lower sides of their buttocks for sitting)
- More sexual dimorphism than Strepsirhines or NWMs
- Visible estrus in females
- Strong dominance hierarchies
- Bilophodont molars (molars form two parallel ridges)

***Figure* $2.8.1$** *- Distribution of Old World Monkeys. Original blank map from http://d-maps.com/carte.php?num_car=3266&lang=en modified world map to show range of Old World Monkeys.*

All OWMs belong to the family Cercopithecidae. They are divided into two subfamilies: Cercopithecinae, monkeys with cheek pouches, and Colobinae, monkeys who are predominately leaf-eaters. There are eighteen genera and about ninety species of OWMs.

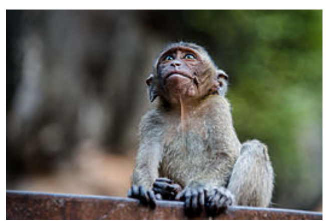

***Figure* $2.8.2$** - *Macaca fascicularis* - crab-eating macaque (notice the nose)

Cercopithecinae

***Figure* $2.8.3$** - Mandrill (*Mandrillus sphinx*)

The largest number of OWM species belong to the Cercopithecinae and include the following genera:

- *Allenopithecus*, i.e., Allen's swamp monkey
- *Miopithecus*, i.e., talapoin
- *Erythrocebus*, i.e., patas monkey

- *Chlorocebus*, e.g., vervet monkey and green monkey
- *Cercopithecus*, e.g., Diana monkey and Pluto monkey
- *Macaca*, e.g., Japanese macaque and booted macaque
- *Lophocebus*, e.g., grey-cheeked mangabey and Uganda mangabey
- *Rungwecebus* i.e., highland mangabey
- *Papio*, e.g., olive baboon and yellow baboon
- *Theropithecus*, i.e., gelada
- *Cercocebus*, white-eyelid mangabeys, e.g., sooty mangabey and collared mangabey
- *Mandrillus*, i.e., mandrill and drill

***Figure* $2.8.4$** - Sexual dimorphism in Hamadryas baboons *(Papio hamadryas).*

There are a number of semi-terrestrial cercopithecines, e.g., baboons, who spend their days foraging in the grasslands and sleep either on cliff-faces or in trees. These semi-terrestrial OWMs exhibit significant sexual dimorphism. Canine teeth are large and sharp; this is beneficial for eating but also for defense against rivals and predators. Ischial callosities are present on the ground-dwelling species. Their faces are bereft of fur except for perhaps a beard-like tuft on the chin. Some have interesting coloration of the face or genitals. Male mandrills (pictured above) have the most conspicuous coloring on their faces and rumps, in addition to their penises, which are bright red. Cercopithecines have elongated snouts with the OWM characteristic noses with nostrils that are narrow and set close together.

***Figure* $2.8.5$** - Japanese macaques *(Macaca fuscata)* in hotspring at Nagano, Japan

Cercopithecines vary in size from the smallest at close to three pounds (*Miopithecus talapoin*) to the largest, the male mandrill (*Mandrillus sphinx*), at about forty-eight pounds. The smaller cercopithecines spend more time in trees than the large cercopithecines. They inhabit a wide-range of environments, from tropical rainforests, e.g., talapoins and mangabeys, to semi-arid deserts, e.g., chacma baboons (*Papio ursinus*), and even areas with seasonal snow, i.e., Japanese macaques (*Macaca fuscata*. In fact, Japanese macaques have an interesting cultural adaptation to living in a cold, snowy region…they hang out in hot springs. Most cheek-pouched monkeys are omnivorous, eating seeds, fruits, leaves, spiders, insects, and even small vertebrates. All cercopithecines live in large multi-male, multi-female groups or single-male, multi-female groups, with bachelor groups forming at times as they migrate from their natal groups. Most females have visible estrus, making it easy for males to tell when the female is fertile. The only species with no to little visible estrus are long-tailed macaques, forest-living guenons, and some mangabeys. Females typically give birth to one offspring at a time.

***Figure* 2.8.6** - Female vervet monkey *(Chlorocebus pygerythrus)* with infant

Colobinae

***Figure* 2.8.7** - Golden snub-nosed monkey *(Rhinopithecus roxellana)*

The Colobinae are quadrupedal folivores, including the colobus monkeys, langurs, and odd-nosed monkeys. There are ten different genera with long tails and various fur coloration:

- *Colobus*, e.g., black colobus and Angola colobus
- *Piliocolobus*, e.g., Zanzibar red colobus and Bouvier's red colobus
- *Procolobus*, i.e., olive colobus
- *Trachypithecus*, e.g., dusky leaf monkey and capped langur
- *Presbytis*, e.g., banded surili and Hose's langur
- *Semnopithecus*, e.g., purple-faced langur and Kashmir gray langur
- *Pygathrix*, e.g., red-shanked douc and gray-shanked douc
- *Rhinopithecus*, e.g., golden snub-nosed monkey and Myanmar snub-nosed monkey
- *Nasalis*, i.e., proboscis monkey
- *Simias*, i.e., pig-tailed langur

***Figure* 2.8.8** - Gray-shanked douc langur *(Pygathrix cinerea)*

Most are arboreal and are found in rainforests, mountain forests, savannas, and mangroves. Because of their leafy diet, colobines have multi-chambered, or sacculated, stomachs to break down plant cellulose into useable calories, and long intestines to increase the absorption of nutrients. They are the only ruminant primates. Colobines are smaller than many of the cercopithecines, weighing from about 10 to 34 pounds. They have short snouts in comparison to the cercopithecines and have teeth that are adapted for shearing leaves. Their legs are somewhat longer than their arms. Colobus monkeys have a vestigial thumb, making fine manipulation of objects impossible. They have little to no hair on their faces other than tufts on the cheeks or chin. All except the snub-nosed monkey have long tails that are used to balance when moving. There is variety in group composition. Multi-male, multi-female groups or single-male, multi-female groups are common; monogamy is rare. Bachelor groups may form as males migrate from their natal group. Females usually give birth to one offspring at a time. During estrus, females have visible menstrual bleeding.

***Figure* 2.8.9** - King colobus *(Colobus polykomos);* note the thumb

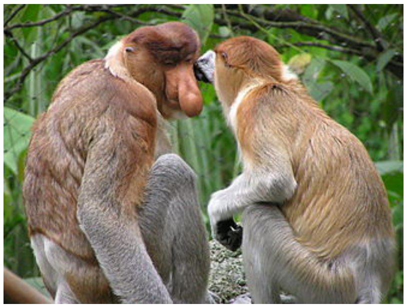

***Figure* 2.8.10** - Proboscis Monkey (*Nasalis larvatus*)

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2.9: Even more Haplorhines (The Apes)

***Figure* $2.9.1$** *- Distribution of gibbons, siamangs, and orangutans. Original blank map from http://d-maps.com/pays.php?num_pay=67&lang=en modified to show distibution of the Southeast Asian great apes.*

***Figure* $2.9.2$** *- Distribution of chimpanzees and gorillas. Original blank map from http://d-maps.com/carte.php?num_car=728&lang=en modified to show the distribution of the African great apes.*

***Figure* $2.9.3$** - Chimpanzee *(Pan troglodytes)* female and offspring

All apes are members of the superfamily Hominoidea; sometimes they are called hominoids. Hominoids are divided into two families: Hylobatidae, the lesser apes, and Hominidae, the great apes. The Hominids are further divided into three subfamilies: Ponginae, Gorillinae, and Homininae, the latter of which is comprised of two tribes: Panini and Hominini. Which apes belong to each of the classifications will be discussed below.

Common Characteristics

Apes share some common characteristics; note these are in comparison to other primates (Jurmain et al. 2013: 142):

- Generally larger body size
- No tail
- Lower back is shorter and more stable
- Arms longer than legs (except for humans)
- Anatomical differences in shoulder joint that facilitate suspensory feeding and locomotion
- Generally more complex behavior
- More complex brain and enhanced cognitive abilities
- Increased period of infant development and dependency

Hylobatidae

***Figure* $2.9.4$** - Siamang *(Symphalangus syndactylus)*

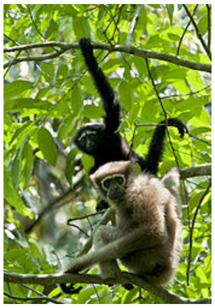

***Figure* $2.9.5$** - Female and male white-browed gibbons *(Hoolock hoolock)*

There is one genera of hylobatids,*Hylobates* and four subgenera: 1) *Bunopithecus*, e.g., Western hoolock gibbon, 2) *Hylobates*, e.g., white-handed gibbon and Bornean white-bearded gibbon, 3) *Symphalangus*, i.e., siamang, and 4) *Nomascus*, e.g., black crested gibbon and yellow-cheeked gibbon, many of which are endangered or critically endangered. They are the smallest of the apes, which is why they are sometimes called the "lesser" apes. Hylobatids rarely spend time on the ground. Because they venture so infrequently to the ground they do not have to contend with predators. "Their lifestyle has enabled them to remain petite and agile" (Hamilton 2006[2]: 222). They are true brachiators. Their arms are much longer than their legs and the thumb is attached to the wrist instead of the palm. This enables them to use their hands as hooks as they swing through the trees. They can move quite fast as their arm span allows them to swing over nine feet in a single movement and they can leap up to almost 30 feet in a single bound (Hamilton 2006[2]). While feeding, hylobatids will use quadrumanous, or four-footed, climbing.

Like some Old World monkeys, hylobatids have ischial callosities, which are for sitting while sleeping (if they do not sit while sleeping, they curl up on their side). They are the only non-human ape that does not build a nest for sleeping. They are well-known for their vocalizations. Monogamous pairs will sing in the morning and evening. The calls can travel over half-a-mile and are used "for territorial defense, maintenance of the pair bond, and general communication" (Paciulli and Neary 2006: 1079). Gibbons may call out 80 to 90% of the day while siamangs only vocalize about 30% of the day. Check out the hylobatids sound gallery from the Gibbons Research Gallery to listen to various vocalizations: http://www.gibbons.de/main/sound.html.

The hylobatids exhibit some sexual dimorphism. They exhibit various colorations as well. For example, female white-browed gibbons (*H. hoolock*) are tan while the males are black; a condition referred to as sexual dichromatism, which means that males and females are different colors. Other species have various color fur, e.g., the silvery gibbon has a silver coat while the Kloss gibbon has a black coat and the Mueller's Bornean gibbon is gray although there is no variation in color between males and females.

Hylobatids are frugivores, although they will eat leaves, flowers and small invertebrates as well. As mentioned previously, they are monogamous and live with their offspring, who may stay with their parents for up to ten years. At some point, offspring "bud off," or take over part of their parents territory and start their own family groups. Families defend their territories, using vocalizations, chasing, and theatrics such as stick breaking and trashing vegetation; rarely are confrontations physical.

Hominidae

***Figure* 2.9.6** - Baby bonobo *(Pan paniscus)*

Orangutans, gorilla, chimpanzees, bonobos, and humans comprise the family Hominidae. Humans will not be covered in this section as Unit 3 is entirely about human evolution. The great apes are the largest primates, with the male eastern lowland gorilla weighing up to 450 pounds. There is extreme sexual dimorphism among orangutans and gorillas; less so in chimpanzees and bonobos. All are quadrupedal, although there are some differences in how quadrupedalism manifests itself. Orangutans exhibit quadrumanous scrambling when arboreal and fist-walking terrestrially while chimpanzees and gorillas are knuckle-walkers. Bonobos also exhibit frequent bipedalism.

Ponginae

***Figure* 2.9.7** - Bornean orangutan *(Pongo pygmaeus)*

***Figure* 2.9.8** - Sumatran orangutan *(Pongo abelii)*

Both species of pongids are critically endangered: *Pongo pygmaeus*, the Bornean orangutan, and *Pongo abelii*, the Sumatran orangutan with dark maroon hair and figure-eight-shaped, hairless faces. Bornean orangutans have ginger-colored hair with light hair on their elongated oval-shaped faces. Bornean orangutans are smaller and fatter than the Sumartran orangs. Second in size only to gorillas, orangutans exhibit sexual dimorphism with the adult males weighing up to 200 pounds with adult females about half that. Mature males have cheek flanges (the bigger the cheek flanges the better as females choose mates based on cheek flange size) and throat pouches with which they make booming calls that alert male rivals and females of their presence. They also have beards and mustaches (Sumatran orangs have longer facial hair than the Bornean orangs). Sexually mature (but not fully grown) males, and occasionally a flanged male, have been known to try to mate with unwilling females, a behavior human researchers have referred to as attempted rape. A study of Sumatran orangs suggests that this is a successful breeding strategy for the unflanged males who sired as many offspring as flanged males without the stress of competing with a fully mature flanged male in an overlapping home range.

***Figure* 2.9.9** - Fully mature male Bornean orangutan *(Pongo pygmaeus)*

Orangutans are solitary primates with males and females coming together only to mate. Females may temporarily socialize with other females, but generally live only with one or two of their offspring. Females usually have one offspring at a time with birth spacing of at least six years. Of the non-human apes, female orangs have the longest period of parental investment, lasting up to ten years. Primatologists suggest that this long period of childcare is so that the young have sufficient time to learn “the complexities of life in the rain forest” (Groves 2006: 1787). Like the hylobatids, orangs spend the majority of their time in trees. Since they weigh too much to walk across tree branches to get to another tree, they return to the ground and walk to the next tree. Sumatran orangutans spend less time on the ground than their Bornean counterparts because they are subject to predators such as tigers and cloud leopards whereas the Bornean orangs do not have the same concern.

Orangutans are frugivores, but also eat bird eggs, termites, caterpillars, ants, bark, sap, and a variety of other foods depending on the season. During mast fruiting (a period occurring every two to ten years when many trees fruit at the same time), orangutans gorge themselves with fruit. This allows the orangs to increase their fat stores. Orangutans spend the majority of their day eating, resting, and moving between trees, upwards to 95% of their day. They spend two to three hours in the morning feeding before resting. In late afternoon they travel before preparing their nest for the night.

One of the major differences between the Sumatran and Bornean orangutans has to do with culture. The former manufacture and use tools. They use leaves for multiple purposes, including umbrellas and “toilet paper.” They use branches as flyswatters and in display behavior. They have been observed modifying sticks so that they can be used to collect insects, open seedpods and large fruits, and dig holes. Stacks of leaves are used as padding when holding spiny fruits.

Gorillinae

***Figure* 2.9.10** - Western Gorilla *(Gorilla gorilla gorilla)*

The “gentle giant” of the great apes, there are two species of *Gorilla*: *G. gorilla* (Western lowland gorilla) and *G. beringei* (mountain gorilla) and four subspecies: *G. g. gorilla*, *G. g. diehli*, *G. b. beringei*, and *G. b. graueri*.

***Figure* 2.9.11** - Male silverback gorilla *(G. beringei)*

Both of the former are critically endangered while the latter is endangered. Gorillas are sexually dimorphic and typically live in single-male, multi-female groups with a dominant male, over twelve-years-old, who has a band of silver-gray hair on its back, thus is referred to as the silverback; however, there are some multi-male, multi-female groups. Both males and females migrate from their birth groups, although female mountain gorillas tend to migrate more than female lowland gorillas, which helps to avoid inbreeding. Also in the mountain gorillas, males may stay with their natal group. When this occurs, the male is subordinate to the silverback and is called a blackback male. If the silverback dies, one of the blackbacks has the opportunity to become the new silverback. For single-male, multi-female groups, when the silverback dies the females and their offspring may disperse to join other groups or they may stay together until a new silverback transfer. Without a silverback to protect the group, infanticide can occur. The silverback maintains bonds with his females through grooming and togetherness. Conflict between silverbacks involves vocalizations and threat displays, including chest beating; rarely is actual physical conflict involved.

***Figure* 2.9.12** - Mountain gorilla *(G. b. beringei)*

Group activity surrounds the silverback who makes all the decisions about when to travel, settling conflict, finding food resources, and defending the group. Blackbacks may assist the silverback with defense. These knuckle-walking primates, spend their days on the ground foraging for food. Females and juveniles sleep in trees, while the dominant male silverback sleeps on the ground. All gorillas are herbivores, although their food focus varies because of their habitats. Mountain gorillas (*G. b. beringei*) are folivores who favor bamboo. Eastern lowland gorillas (*G. b. graueri*) eat seasonally, focusing on fruit when available. They will also eat ants. Western lowland gorillas (*G. gorilla*) also focus on fruit, but also eat herbaceous vegetation, termites, and ants. Because of their diets, the home range of gorillas varies, with Western lowland gorillas having the largest range and mountain gorillas the smallest.

Females usually give birth to one offspring at a time. Infant mortality is high among mountain gorillas (up to 38%) so the mother's care is particularly important. Males are involved in socialization of infants but do not provide care beyond protection. Infants are weaned after three or four years, providing a decent interval between births and increasing the infant's chance of survival.

Homininae

***Figure* 2.9.13** - Adult female and infant wild chimpanzees *(Pan troglodytes)* feeding on *Ficus sur* (figs)

There are two genera of extant hominins: *Pan* and *Homo*, with two species of *Pan*: 1) *Pan troglodytes* and 2) *Pan paniscus*, and one species of *Homo*: *Homo sapiens*.

The endangered *Pan troglodytes*, common chimpanzees, and *Pan paniscus*, bonobos are the apes most genetically similar to humans (98%+). Some researchers (Grove 2001 and Wildman et al. 2003) argue that chimpanzees are so closely related to humans that they should be genus *Homo*.

***Figure* 2.9.14** - *Pan paniscus (*note the part in the hair*)*

Chimpanzees live in West and Central Africa, primarily in Gabon and the Democratic Republic of Congo. They inhabit a number of habitats, including, savannas and montane, swamp, and evergreen rainforests. Bonobos are found only in the Democratic Republic of Congo in closed-canopy rainforest. Both chimps and bonobos exhibit some sexual dimorphism. Male bonobos weigh on average 86 pounds and females 63 pounds. Male chimps are slightly larger at an average of 88 to 132 pounds, and females between 70 and 104 pounds; they are sturdy and strong. As indicated by the average weights, chimpanzees are somewhat larger than bonobos. Chimpanzees have black hair and are born with pale faces that darken as they age. Males and females have beards and prominent ears. Bonobos have black fur and black faces with hair tufts on the sides of their faces and a part in the hair on their heads. While both species are quadrupedal knuckle-walkers, both can walk bipedally (although bonobos are better bipedal walkers) and bonobos also semi-brachiate.

Chimpanzees live in multi-male, multi-female groups, ranging anywhere from ten to over one hundred individuals. The core of the group is centered on an alpha male along with a small group of bonded males, although in West Africa, some groups appear to be oriented on females. The alpha male and his subordinates use physical force, display behavior, and aggression to control the community. They work together to defend the group's territory, patrolling and chasing out unfamiliar males. The size of the group's territory is dependent on the number of males in the group. Even though this small group of males works with the alpha, the dominant chimpanzee must constantly work to maintain his position of power.

***Figure* 2.9.15** - Mother chimpanzee *(Pan troglodytes)* and offspring

The strongest bond within chimpanzee social groups is between mothers and their offspring. Females generally have one baby at a time and give birth approximately every five to six years. Even though offspring are weaned by the time they are three-years old, juveniles may stay with their mother and siblings until age five through eight and help with childcare. Juvenile females leave the group at about ten-years-old, except for those groups that are centered on a core group of females. There is quite a bit of movement among group members who do not always spend the day together; they often break off into smaller groups of three to six individuals to forage.

Chimpanzees are omnivores, eating fruits, resin, bark, young leaves, tree seeds, and pith (Orcholl 2006). They incorporate over 300 species of plants in their diet. Some plants seem to be used only for medicinal purposes. Chimpanzees also incorporate animal protein in their diet, which comes from small mammals, including other primates like the colobus monkey, and insects such as termites. Male, and the occasional female, chimpanzees use cooperative techniques to hunt (watch this short video of chimps on the hunt: youtu.be/A1WBs74W4ik). At Mahale Mountain National Park, Tanzania, researchers have observed several occurrences of infanticide after failed hunts. Chimpanzees have been documented making and using spears to hunt and "fishing sticks" to acquire termites and honey (you can check out this short video about spear-wielding chimps: youtu.be/FyGxQq7jSA8). Chimpanzees have other cultural behaviors, including the hand-clasping grooming technique, using wadded up leaves as sponges, and hammers and anvils to break open nuts.

***Figure* $2.9.16$** - Bonobos *(Pan paniscus)*

Bonobos are sometimes referred to as pygmy chimpanzees because they are slightly smaller and more slender than common chimpanzees, but the weight differences, as mentioned above, are not that great. There is less sexual dimorphism than chimps and about the same as in humans. Bonobos are efficient bipedal walkers and have been documented wading in streams while fishing, walking while carrying an armload of sugar cane, and with arms over each other's shoulders (Orcholl 2006).

***Figure* $2.9.17$** - Bonobo *(Pan paniscus)*

Bonobos live in fission-fusion social groups of over twenty individuals. Mother and son bonds are the strongest as sons use their mother's rank in the social hierarchy as a means to garner favor with other high-ranking females. It is usually the highest-ranking female's son who is alpha, but the alpha position is much different than that of the chimpanzee. The male and female alphas are almost equally dominant (Orcholl 2006). Unrelated females (juvenile females leave their natal group between ages seven to nine) work together to protect their offspring and secure resources at the expense of males. There is no core group of males that work together---after the alpha male, the hierarchy of males is murky. Also unlike chimpanzees, physical aggression is rarely used to dominate and intimidate. Intra-group conflict is settled using sexual interactions such as rump-rubbing and penis fencing among males and genital-to-genital rubbing (G-G rubbing) among females. Females wishing to join a group will use G-G rubbing with the alpha female and intercourse with the alpha male to gain admittance. While to humans, this might seem like an unusual ways to use sexual behavior, these behaviors, along with the fact that female bonobos are always receptive to sexual contact, have multiple partners, and copulate while pregnant, has eliminated infanticide from bonobo society. The fact that females leave their natal groups prevents incest. Females usually give birth to a single offspring; birth-spacing is from four to six years. Because males do not know which offspring belong to them they do not invest their time in infant care. Mothers are solely responsible for their offspring, which may help to explain why females band together.

Unlike chimpanzees, bonobos do not make and use tools, although captive bonobos have been observed using objects that are made available to them, such as tennis balls as water sponges. They do, however, exhibit emotions such as sympathy and empathy. They seem to respect other individuals' privacy, never entering another bonobo's sleeping nest. Like chimps, bonobos use at least one plant for medicinal purposes, specifically a leaf used when they have an intestinal parasite. Bonobos are omnivores, although about 57% of their diet is from fruit. They also eat leaves, flowers, bark, pith, roots, mushrooms, sprouts, and seeds. While bonobos do not hunt, they will opportunistically eat small mammals, insect larvae, earthworms, honey, eggs, and soil (Orcholl 2010[1]). Finding a food source can set off a flurry of excitement and sexual interaction.

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2.10: Primate Evolution

***Figure* 2.10.1** - Fossil ape*: Proconsul*

Now that you have an understanding of living primates' morphology and behavior, it is time to learn about the origins of primates. the study of primate evolution is multidisciplinary in nature and incorporates data and methods from paleontology, geology, anthropology, and archaeology to study the fossil record of primates.

Fossils

***Figure* 2.10.2** - *Permineralized wood*

Fossils are at the center of the study of ancestral primates. Animal fossils provide insight into morphology and behavior of ancient organisms while plant fossils help paleoanthropologists reconstruct ancient environments (paleoecology). One thing to keep in mind is that, "the fossil record is highly skewed in favor of organisms that died and were preserved in calm seas, estuaries, tidal flats, or the deep ocean floor (where there are few scavengers and little disruption of layers)" (Panell 2014: 1839). There are multiple ways that fossils form. Permineralization, or petrification, is the most common process. This occurs when organic remains decay and water seeps into the remains and deposits minerals that form crystals which harden. Generally, it is the bone that is fossilized as they are the hardest parts of the body and take the longest to decay, giving time for the minerals to crystalize and harden. Fossils can also form when an organic entity is encased in tar, resin, or even ice. When this occurs bodily tissues can be preserved, but it as extremely rare occurrence. Carbonization can lead to fossilization as well. When an organic item is buried in sediment, heat and pressure causes the release of hydrogen and oxygen, which leaves behind a carbon residue. To read more about other methods, check out the article, "How Do Fossils Form?" You can also learn more about the fossilization process by watching this short video, Becoming a Fossil.

When a fossil is found, it can be dated using a variety of methods. Some methods date the fossil itself; other methods use the surrounding matrices. There are relative dating techniques that provide an order of occurrence, but no absolute dates, and there are absolute, or chronometric, dating techniques that provide dates (usually a range of dates) for an object. Examples of relative dating techniques include stratigraphy, index fossil concept (biostratigraphy), and flourine dating. Stratigraphy involves mapping observable geologic strata and the artifacts (e.g., fossils) included in those layers. Building on stratigraphy, index fossils are used as time markers. Let's say that one type of fossil was found in a strata at Site A and the same type of fossil was found in a strata at Site B, then we can assume that the strata and fossils at both sites were deposited at the same time. Flourine dating is a process that uses the amount of flourine accumulation as a basis for comparison between objects, e.g., if two objects have similar amounts of flourine then they were most likely deposited at the same time. Radiometric techniques are commonly used for dating fossils.

Radiocarbon (^{14}C-dating) was the first radiometric dating technique developed; it revolutionized anthropological studies of the past. ^{14}C-dating can be used on organic materials and is accurate to about 70,000 years ago. It measures the rate of decay of carbon-14. Fission tracking involves measuring the track density of decaying uranium-238. As this method works best on igneous materials, it can be used to date the matrix surrounding fossils. Potassium-Argon dating (K/Ar-dating) is employed frequently in the study of primate origins. This method measures the rate of decay of potassium-40 into argon-40. Again, the rock surrounding fossils is dated and not the fossil itself. These are just a few of the dating methods used. You can learn more about these and other dating methods by reading the article, "Dating Rocks and Fossils Using Geologic Methods" (optional).

Taphonomy

The study of what happens to organisms after they die is called **taphonomy**. Taphonomic studies of fossils is important in order to understand the context of the fossil and the environment from which it came. Has the fossil been disturbed in any way? Has it been moved by water, scavenged by animals, etc?

Sometimes taphonomy is done with experimental methods.

Paleoecology

Paleoecologists study "...the physical structure and biological functions of organisms, their interactions with other, and their role in ancient ecosystems" (Lerner and Lerner 2014: 3217) to determine what the landscape may have looked like during the time that a particular organism, including primates, lived there (remember, evolution is environmentally dependent!). There are several specialized areas of study within paleoecology. **Paleobotany** is the study of fossil plants. For more on paleobotany, check out Dr. Robert Gastaldo's site: A Brief Introduction to Paleobotany. **Paleopalynology** is the study of fossil pollen while **phytoliths** are fossilized plant cells.

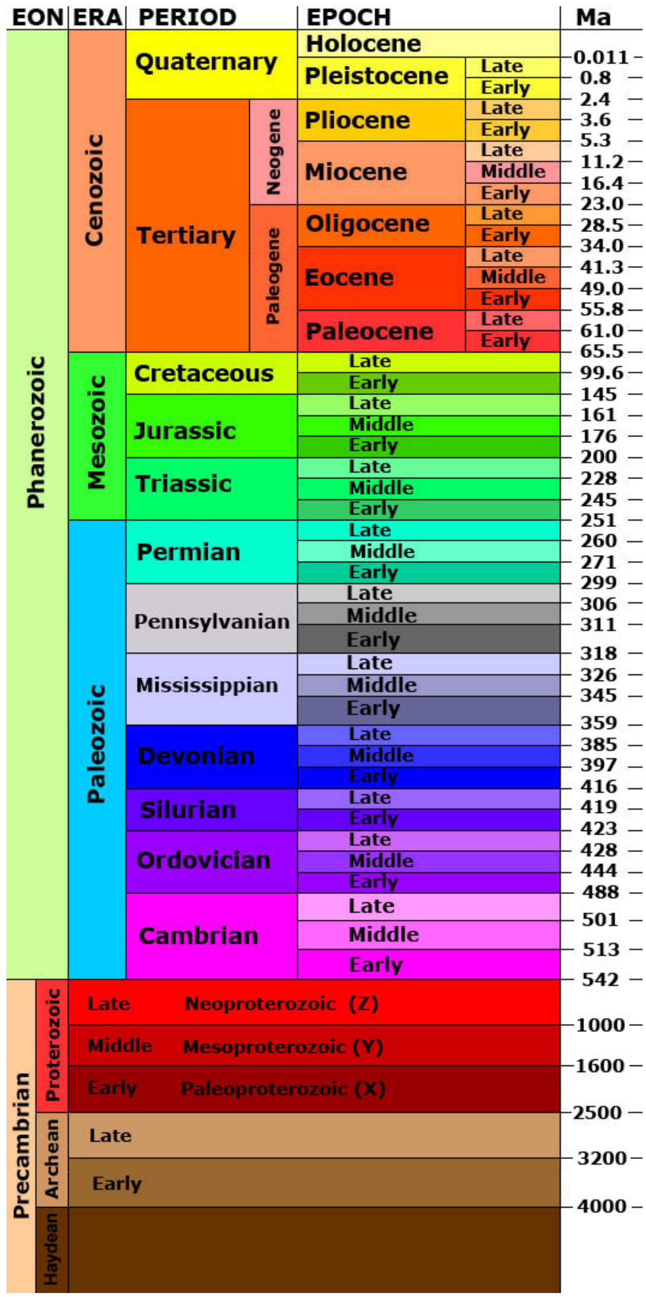

***Figure* 2.10.3** - *Geologic time scale*

Geologic time

From geology we have an understanding of the time involved in the development of earth. In biological anthropology, we are specifically focused on the late Mesozoic/early Cenozoic eras in relation to primate evolution. You should be familiar with the time ranges for the epochs of the Cenozoic. Below you will learn about primate developments associated with each epoch.

If you are feeling particularly investigatory today, you may want to check out this interactive geological time machine (optional)

Primate Evolution

The Mesozoic: the origin of mammals

The Mesozoic era is known as "the age of the dinosaurs" due to their ecological dominance at the time; however, it is during this era that the first mammals evolved, including a primate-like mammalian ancestor. Research using DNA analysis and fossils suggests that by 75 mya (million years ago) all of the mammalian orders had diverged. The various mammalian families began to diversify in the Cenozoic era (Jurmain et al. 2013).

Several things happened at the end of this period that led to a rise in the mammals:

- a rise in the number and diversity of **angiosperms** (flowering plants)
- the K-T boundary extinction

The Cenozoic era

The Paleocene epoch

Proto-primates, primate-like mammals, evolved in the Paleocene epoch, about 65 mya. The proto-primates from this epoch are controversial; some argue that they are related to primates but are not actually primates (hence, "proto-primates"). The strongest evidence linking these proto-primates or Plesiadapiformes to primates comes in the form of *Carpolestes simpsoni*, a pleasiadapid found in Wyoming, USA. This fossil species has an opposable big toe, grasping fingers, and nails instead of claws (Bloch and Boyer 2002).

***Figure* $2.10.4$** - *Plesiadapiformes: Plesiadapis*

Plesiadapiformes Overview

- Flexible body, some had nails (not claws), bushy tail
- Small brain, **prognathic** face (projecting or snout-like). **diastema** (gap) between the incisors and the premolars
- Similar in lifestyle to an opossum, ate fruit and insects
- Found in North America and Europe (which were connected during this time period)
- Ranged from mouse-sized to small monkey-sized (11 lbs)

To learn more about the Plesiadapiformes, watch this optional short film: First Primates. Still want to learn more? Check out "Primate-like Mammals: A Stunning Diversity in the Treetops" (optional).

The Eocene epoch

The Eocene epoch (56-33 mya), with its warmer and wetter climate and adaptive radition of rainforests and angiosperms, sees the emergence of the first true primates, also called euprimates. Bloch and Boyer (2002) suggest that*Carpolestes* is ancestral to the euprimates. Over two hundred Eocene fossil primate species have been identified (Jurmain et al 2013). The euprimates are about the same size as modern squirrels, with prehensile hands and feet and more forward-facing eyes that gave them stereoscopic vision. These earliest primates are most like the strepsirhines and have been found in North America, Europe, North Africa, the Middle East, and Asia, which were all still connected during this time frame. Based on the fossils that have been discovered to date, we can suggest that Eocene primates were (Jurmain et al. 2013: 189):

- widely distributed
- mostly extinct by the end of the Eocene
- most are not ancestral to later primates

There are two main families of Eocene primates:

- Adapids: ancestor of strepsirhines
- Omomyids: ancestor of haplorhines

Adapids

***Figure* 2.10.5** - *Adapid*

- Found in North America, Europe, Asia, and Africa
- Resemble lemurs
- Forward-facing eyes, larger brain, less prognathic
- Nails (not claws), opposable thumb (and big toes)
- Flexible body
- Ate more leaves

Most recently, the discovery of *Darwinius* fossils in Messel, Germany will help to shed light on the evolution of the euprimates. *Darwinius*, dated to 47 mya, is the most complete fossil found from the Eocene. *Darwinius* appears to be a transitional adapid ancestor to monkeys and apes, which contradicts what most researchers claim that omomyids are the ancestors of monkeys and apes. As researchers other than the discoverers have opportunities to study the fossil, more will be made clear.

Omomyids

***Figure* 2.10.6** - *Omomyid*

- Found in North America, Europe, and Asia
- More closely resemble noctural prosimians, especially tarsiers
- Largest are around 1 kg
- Nails (not claws)
- Less prognathic, big eyes (close together), larger brain
- Ate more fruits and insects

The Oligocene epoch: the monkey/ape divergence (34 to 23 mya)

The global climate shifted again, cooling and drying, during the Oligocene epoch (33-23 mya). There is a reduction in the amount of rainforests, which retreated toward the equator, but an expansion of grasslands. So, there was an increase in **terrestrial** (ground) niches and a decrease in **arboreal** (tree) niches. While most of the fossils from this time are Old World monkeys, some are ancestors of New World monkeys; at this point the American continents had separated from Africa and Eurasia.

Parapithecids

- A good example of these was *Apidium*
- Size of squirrel, but more monkey-like
- **Quadruped** (walked on all fours)

- Dental formula 2-1-3-3 (so is possibly the **platyrrhine** or New World monkey ancestor)

Propliopithecids

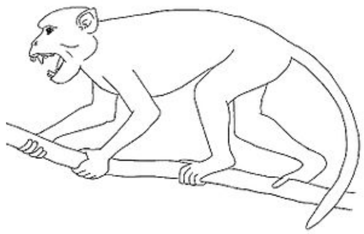

***Figure* 2.10.7** - *Aegyptopithecus*

- A good example of these was *Aegyptopithecus* (pictured right)
- More ape-like
- Dental formula 2-1-2-3 (so is possibly the **catarrhine** or Old World monkey and ape ancestor)
- Aegyptopithecus in the news!

More on the origins of New World Monkeys: The Origins of Platyrrhine Monkeys in South America

The Miocene epoch: the Old World monkey/ape divergence (23 to 5 mya)

There were two climate shifts during this period, first there was a warm period with heavy forestation, followed by drier and cooler climates with decreasing forest and increased grasslands.

At this point, the Old World monkeys and apes split within the catarrhines. The fossils are from east Africa.

The ape ancestors had the following traits:

***Figure* 2.10.8** - *Sivapithecus*

- no tail
- arboreal quadrupeds (limb structure was still monkey-like)
- y-5 molars
- Some good examples of these are: *Proconsul*, *Sivapithecus* (pictured right), *and Gigantopithecus*

The Old World monkey ancestors at this point in time had the following traits:

- A tail
- Had macaque-like faces
- Were medium sized 7-11 lbs
- A good example of these is: *Victoriapithecus*

Where did primates come from?

There are three primary hypotheses about the origins of primates. The earliest hypothesis, the arboreal hypothesis, claims that the first primates evolved a suite of traits for living in trees, e.g., grasping hands and feet and stereoscopic vision. This hypothesis held sway from the early 1900s until the 1970s when the visual predation hypothesis was proposed. This hypothesis suggests that primates evolved because they provided an advantage for hunting small insects, e.g., orbital convergence that allowed for 3d-vision. Shortly thereafter, the angiosperm hypothesis was proposed, which claims that primate evolution is related to the adaptive radiation of angiosperms or flowering plants. Each of these hypotheses have been challenged over time, and it may be that each may play a part in explaining primate evolution. For more details on these hypotheses, you can check out this short article [optional]: The Origin of Primates.

In 2010, a controversial new hypothesis was proposed by Michael Heads. Heads suggests that volcanic eruptions and the breakup of the super continent, Pangea, lead to the emergence of the different lineages of primates. You can read more about Heads' hypothesis on LiveScience [optional].

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CHAPTER OVERVIEW

III: Human Evolution

Learning Objectives

At the end of this unit, students will be able to:

- define the basic Trends of human evolution: Bipedalism & Big Brains
- distinguish the Early hominins
- describe The genus Homo: Early Homo & Modern Humans
- relate Material & Aesthetic culture to hominin evolution

In the last unit, students investigate the origins of bipedalism, encephalization of the brain, and the evolution of hominins.

Thumbnail: The original complete skull (without upper teeth and mandible) of a 2,1 million years old Australopithecus africanus specimen so-called "Mrs. Ples" (catalogue number STS 5, Sterkfontein cave, hominid fossil number 5), discovered in South Africa . Collection of the Transvaal Museum, Northern Flagship Institute, Pretoria, South Africa. (CC BY-SA 4.0; José Braga; Didier Descouens).

3.1: Trends

Paleoanthropologists are trying to answer a number of questions about human evolution.

- Why did our earliest ancestors stand up?
- How did our ancestors provision themselves?
- Why did some species become extinct until only one species, *Homo sapiens*, was left?
- When, where and why did modern humans evolve?
- What was the role of the Neandertals?
- What makes us human?

While hypotheses have been suggested, new research continues to change and hone the picture of the evolution of humanity. This section of the course is not intended to provide a complete review of paleoanthropological research, but merely to provide an overview of key finds and outline trends in hominin evolution. For more in depth information, please see the "For Further Exploration" at the end of this page.

***Figure* 3.1.1** - *Paleoanthropologist Don Johanson*

You may want to start with a 15-minute video by Louise Leakey Digging for Humanity and for a little bit of fun, check out The Simpsons take on evolution, both biological and cultural!

Morphological Trends in Human Evolution

There are a number of trends in the evolution of the proto-hominins to modern *Homo sapiens*. These traits do not occur all at once, but over millions of years. In general, the trends include:

- the forward movement of the foramen magnum
  - a reduction in the size of the canines
  - an increase in the size of the molars
  - disappearance of the diastema (gap between the incisors and canines)
  - an increase in cranial capacity
  - a decrease in prognathism (jutting forward of the bottom part of the face)
  - thinnng of the bone
  - rounding of the skull

Again, not all of these traits occur at the same time and there is variation among the various hominin species, but all of these morphological characteristics occur in the evolutionary line of *Homo sapiens*. More details will be given about these traits in the sections on the hominins. Three other trends are important in the evolution of hominins:

- bipedalism,
- non-honing chewing complex, and
- encephalization of the brain.

These are discussed in more detail next.

Bipedalism

For a long time, paleoanthropologists thought that large brains were the first hallmark of becoming human; however, research in the 20th century showed that bipedalism, or upright walking, was the first morphological trait on the road to humanity. Human bipedalism differs from the bipedalism practiced by other primates in that it is habitual. In other words, it is the primary form of moving around. Other primates practice **facultative bipedalism**, which is a temporary form of bipedal locomotion, e.g., primates like chimpanzees may walk bipedally while they carry something in their hands. Few other animals are habitual bipeds, e.g., birds and kangaroos.

Figure $\mathbf{3.1.2}$ - *Human skeleton walking*

There are numerous anatomical changes that evolved to make hominins efficient bipedal locomotors. Here are some, but not all, of the major changes that occurred (eLucy 2007):

- foramen magnum: the foramen magnum is the hole at the bottom of the skull, allowing for the spinal cord to pass through perpendicular to the ground
- spinal cord: the s-shape of the spine lowers the center of gravity needed for efficient bipedal walking
- lumbar vertebrae: hominins have five lumbar instead of four like gorillas, which are also larger than those of gorillas, allowing for more flexibility in the lower back which in turn allows the hips and trunk of the body to swing forward
- pelvis: the pelvis became bowl-shaped to help support the upper body while walking, aid in balance, and provide for the necessary muscle attachment that allows for the forward swing of leg; the hip joint is larger than other apes to help with stress absorption; the ilium has a more lateral orientation that helps prevent the leg that is on the ground during walking from collapsing toward the swinging leg; wider hips help with maintaining the center of gravity
- femur: the larger femoral head along with the hip joint absorbs more stress while walking; femur, along with the knee joint, is angled toward midline of hip to help with balance--the angle is called the bicondylar angle (this is sometimes called being "knock-kneed")
- knee: the knee joint, or valgus knee, is closer to the midline of the hip to help with maintaining balance while walking upright
- tibia: placement is almost directly parallel with center of gravity
- feet: big toe, or hallux, is inline with other toes, which allows for more force when pushing off while walking; the heel bone is robust, which helps with shock absorption and stability--it also allows the attachment of strong ligaments from the ankle to the foot that form a double arch, helping with shock absorption

The morphological changes associated with bipedalism take millions of years to evolve. They first appear with the proto-hominin *Sahelanthropus tcahdensis*, which is dated to 6.0-7.0 million years ago (mya), but are not fully in place until around 4.0 mya. These physical changes continue to refine until we see them as we do today in modern Homo sapiens (Jurmain et al. 2013).

You can explore all of the anatomical changes associated with bipedalism in more detail by visiting Step by Step: The Evolution of Bipedalism hosted by the Department of Anthropology at The University of Texas-Austin [optional].

Hypotheses on the Evolution of Bipedalism

Several hypotheses have been proposed over the last century or so to explain the evolution of hominins. As bipedalism is the first trait on the road to modern humans, these hypotheses focus on the emergence of habitual bipedalism. Many have been refuted as new data is discovered. The first hypothesis was the hunting hypothesis proposed by Charles Darwin. The hunting hypothesis claims that the key to human evolution was the shift from an arboreal life to a terrestrial one. He predicted that the earliest hominins would be found in Africa based on the similarities he saw between humans and African apes. He suggested that bipedalism gave the first hominins an advantage in that it freed up their hands to carry weapons used to hunt animals. Darwin also suggested that larger brains preceded bipedalism as intelligence was needed to make the tools. Now we know that habitual bipedalism predates large brains so Darwin's hypothesis is no longer considered an adequate explanation. With the discovery of new data, other hypotheses have been proposed including the patchy-forest and provisioning.

The patchy forest hypothesis suggests that the emerging mosaic environment that began emerging at the end of the Miocene made bipedalism advantageous. The phrase mosaic environment in this case refers to an environment that had patchy forest interspersed with grasslands that eventually became the African savannas that we know today. This caused food resources to become spread out over the landscape. For traveling long distances, bipedalism is more energy efficient than quadrupedalism. Traveling bipedally freed up hands for carrying provisions and the early hominins could have easily fed from both terrestrial and arboreal resources.

The provisioning hypothesis states that having hands free to carry food allowed males to provision females and offspring. Since much of the females energy went to child-rearing, the ability of a male to provision her and her offspring would have been an attractive quality. Those males who could walk more efficiently bipedally while carrying food would have been prime mate material, allowing both the male and female to reproduce successfully.

The truth of the matter is that the origins of bipedalism are still murky. Further research will hopefully help us come closer to a determination of why bipedalism, and hence our early ancestors, evolved. In the meantime, you can explore other hypotheses on the origins of bipedalism on the NOVA web site: http://www.pbs.org/wgbh/nova/evoluti...ipedalism.html [optional].

Non-honing Chewing Complex

Apes have a honing chewing complex, which is good for cutting and shredding food. Their upper canines are large, pointed (triangular shape), and projecting. These two teeth also have a sharp edge on the back. This edge is kept sharp because each time the jaws close, the upper canine rubs against, or hones, the sharp edge of the lower third premolar. This can happen because of the diastema present on the jaws that allows for the jaws to close completely. Without the honing action, the canines and premolars would not be able to efficiently shred leaves and fruit.

Over time, hominins lose this honing complex. The diastema disappears, the canine reduces in size, and the molars increase in size (Larsen 2014).

Encephalization of the Brain

Encephalization of the brain refers to a couple of things: 1) the increase in brain size over time and 2) the size of the brain in relation to total body mass. The brain-size to body mass ratio does not change that much in the hominins. "The stature of *A. afarensis* varied from 3.3 to 5 feet (1 to 1.5 meteres) tall, while that of modern humans varies from approximately 4.5 to over 6 feet (1.4 to 1.8 meters)" (Campbell and

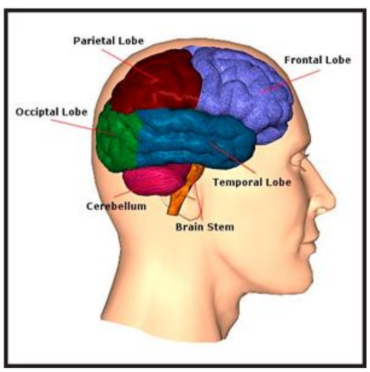

***Figure* 3.1.3** - *Parts of the brain*

Loy 2000: 285). However, while there is gradual increase in brain size throughout the australopithecine lineage, it is not until early *Homo* that there is a significant increase in cranial capacity, approximately a 20% increase over australopithecines. More significantly is the approximately 50% increase in brain size of *Homo erectus* and the earlier *Homo* species. It is not just the size of the brain that is important. During this process of encephalization, there is also a rewiring of the brain that coincides with the emergence of material culture such as stone tools. It is not until this occurs that hominins leave Africa, enabled greatly by cultural advances.

Non-human primate brains are symmetrical as are the brains of early hominins. With the emergence of *Homo* we see the lateralization of the brain--it becomes asymmetrial (right brain, left brain). We know this from endocasts. Endocasts form when minerals replace brain matter inside the cranium during the fossilization process. These endocasts allow paleoanthropologists to study the cortical folds of the brain and compare it to modern humans. Based on endocasts, researchers determined that three areas of the brain began to change in *Homo*: the cerebellum, which handles learned motor activities, the limbic system, which processes motivation, emotion and social communication, and the cerebral cortex, which is responsible for sensory experiences. It is these changes that may have allowed the early members of our genus to develop cultural adaptations to environmental pressures.

Why did the brain change in early Homo?

The question that confronted paleoanthropologists was why the brain changed. Big brains have some disadvantages:

- it take approximately 25-30% of a human's metabolic energy to run their brain
- requires infants to be born prematurely, resulting in a longer period of infant dependency (the average infant brain is about 1/3 the size of an adult brain)
- longer infant dependency is an increased drain on maternal energy; the mother must have proper nutrition not only for herself but for the nursing infant
- it has been suggested that larger brains decrease the bipedal efficiency of females because they must have a wider pelvis and birth canal to give birth to a large brained infant

So, for large brains to become fixed in the *Homo* population, the advantages had to outweigh the disadvantages listed above.

One possible explanation incorporates the interaction of three different variables: group size, complex subsistence patterns, and the nutritional value of meat (Campbell and Loy 2000: 318). Let's address group size first. Research suggests that brain size and size of social groups correlates positively among living primates, implying that big brains helped individuals keep track of such things as dominance hierarchies, allies, etc. Second, a big brain allows for primates to keep track of large subsistence territories and allows for omnivores to develop strategies for collecting a wide-variety of foodstuffs. Third, eating meat is a relatively easy way to get the nutrition needed to run a big brain, which, as mentioned above, in modern humans takes about 1/3 of our daily metabolic energy. The argument for this, the social brain hypothesis, is laid out by Robin Dunbar in this [psych.colorado.edu/~tito/sp03/7536/Dunbar_1998.pdf article]. Dunbar also claims that it was changes in the neocortex, a 2-4mm thick top layer of the cerebral hemispheres, that were critical in the "hominization" (development of cognitive abilities) of our ancestors. Please read this short article on the evolution of human cognitive abilities.

Geology & Environmental Background

The Miocene period (roughly 23-5 million years ago) was geologically active in Africa. This is the period of the adaptive radiation of the apes and a period of mountain building that led to the formation of the Great Africa Rift Valley (see Image: Great Africa Rift Valley). With the emergence of the rift mountains, the rains that heretofore had moved across the continent from the Atlantic Ocean were blocked (referred to as a rain shadow), leading to the aridification of Eastern Africa (Image: African Rift Valley, Kenya and Image: Rift Valley, Afar, Ethiopia). The savanna environment that evolved in Eastern Africa was and is a much more open environment than the forested environment of Western and Central Africa, leading to rise of new adaptations for plants and animals. It is in this newly emerging environment that hominin evolution takes off, although recent research indicates that proto-hominins lived in Western Africa.

Paleoclimatic data has been correlated with speciation events in hominin evolution, but it does not seem to account for all speciation events. Paleoanthropologists are still working to identify the selective pressures that resulted in the evolution of different hominin species. Nonetheless, the paleoclimatic data suggests the following:

- Grasslands spread in Africa between 10-5 million years ago during a cooling and drying phase. It is during this time frame that the common ancestor of African apes and humans lived. The common ancestor was more than like a quadruped who was arboreal or at least spent a significant amount of time in the trees. In the middle of this period, approximately 7-6 million years ago, the first bipedal hominin emerged, *Sahelanthropus tchadensis*. *Sahelanthropus* and a few other early hominins are referred to as proto-hominins in recognition of their primitive, ape-like features.
- In the mid-Pliocene period, 3-2 million years ago, yet another cooling and drying phase is correlated with the adaptive radiation of the hominins, including the emergence of the robust australopithecines (note: some paleoanthropologists place these species in a separate genus, *Paranthropus*. In this course we will refer to the robust species as *Australopithecine*) and the genus *Homo*.
- Near the beginning of the Pleistocene period, also known as the Ice Age, the environment continued to get drier. Open habitats spread in East Africa. During this period, *Homo ergaster* (*Homo erectus*) emerges and finally leaves the African continent.

This data has a tendency to make us think that hominin evolution was driven by environmental changes; however, the presence of *Sahelanthropus tchadensis* in West Africa forces paleoanthropologists to acknowledge the possibility that geologic, climatic, and environmental changes occuring in Africa during the Miocene, Pliocene and Pleistocene had little to do with the evolution of hominins.

For Further Exploration

Explore Human Evolution in Print

- Boyd, Robert and Joan B. Silk. 2009. How Humans Evolved, 5th edition. New York: W. W. Norton.
- Campbell, Bernard G. and James D. Loy. 2000. Humankind Emerging, 8th edition. Boston: Allyn & Bacon.
- Johanson, Donald and Kate Wong. 2010. Lucy's Legacy: The Quest for Human Origins. New York: Harmony Books.
- Stringer, Chris and Peter Andrew. 2006. The Complete World of Human Evolution. New York: Thames & Hudson.
- Tattersall, Ian. 2008. The Fossil Trail: How We Know What We Think We Know About Human Evolution. New York: Oxford University Press.

Explore Human Evolution on the Web

- Becoming Human
- Talk Origins Fossil Hominids
- Hall of Human Origins
- Science Daily: Human Evolution News
- Rediscovering Biology:Unit 9 Human Evolution
- BBC: The Evolution of Man
- Human Evolution: The Fossil Evidence in 3d

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3.2: Proto-Hominins

In determining what fossil features denote a specimen is a hominin, many different characteristics are examined, including those related to bipedalism, about which you previously learned, and non-honing chewing. Apes have a canine-premolar honing complex, which means that there is a diastema between the lower canine lower third premolar where the upper canine fits when the jaws close (Larsen 2014). Other characteristics such brain and body size and what, if any, cultural behaviors are associated with the fossil remains are also scrutinized.

The various features associated with hominins developed at different rates, a situation referred to as **mosaic evolution**. In determining which species a fossil specimen belongs to, paleoanthropologists utilize comparative anatomy. There is much discussion among researchers as to the exact number of species. Some tend to see broad ranges of variation, which results in fewer species. Researchers with this approach are sometimes referred to as "lumpers" because they lump fossil specimens in relatively few species. Other researchers see more narrow ranges of variation and are referred to as "splitters" because they see more variation of species in the fossil record. For the purposes of this course, we are going to use the approach presented in Jurmain et al. (2013), which is more of a lumper approach.

While the hominins will be presented more or less in chronological order, do not mistake chronological order for linear evolutionary relationships; some hominins that are presented are not in the direct line to modern humans. It is also important to keep in mind that new discoveries are made each year that refine what we know about human evolution. What this means is that what you learn this quarter could change somewhat next year as new data is made available. While this can make studying human evolution frustrating at times, the new discoveries help us gain a better understanding of just how our early ancestors evolved.

It is highly recommended that you begin your exploration of human evolution by watching the documentary, Becoming Human.

Proto-hominins

Sahelanthropus tchadensis

Discovered by the Mission Paléoanthropologique Franco-Tchadienne (MPFT) led by Michel Brunet at Toros-Menalla, Chad, during the 2001-2002 field season, ***Sahelanthropus tchadensis*** is the oldest hominin discovered to date. Cosmogenic nuclide dating (https://en.Wikipedia.org/wiki/Surface_exposure_dating) places *Sahelanthropus* between 7.2 to 6.8 mya (million years ago) (Lebatard et al. 2008). The binomial recognizes the area where the fossils were found, Sahel. The type specimen, also referred to as a **holotype**, includes "…a nearly complete cranium and…parts of two mandibles and some isolated teeth" (Bailey 2006: 2044).

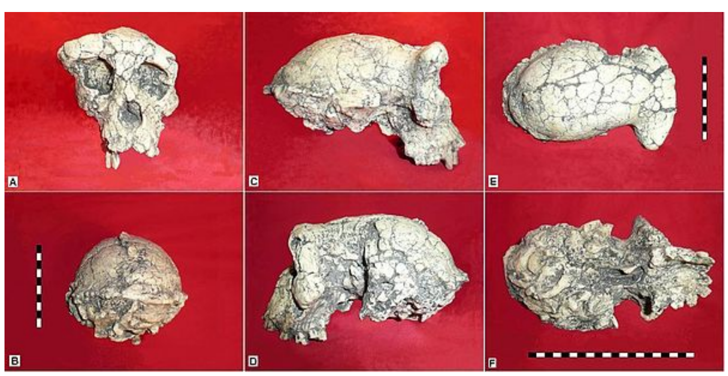

Figure 3.2.1 - *Sahelanthropus tchadensis*

The skull is a combination of ape-like and human-like features. Ape-like features include brain size, heavy brow ridge. Its human-like features include forward position of the foramen magnum (visit http://www.nature.com/scitable/knowl...hecus-67648286 (scroll down) to view image comparing placement of foramen magnum in chimps, humans, and *Sahelanthropus*), reduced prognathism, smaller canine teeth, and intermediate thickness of the premolar and molar enamel. Due to the pronounced brow ridge Brunet's team suggests that the *Sahelanthropus* specimen is male.

There is debate among researchers as to whether *Sahelanthropus* is a hominin or an ape. Some suggest that the specimen belongs to that of a female ape because it is likely to find canines worn at the tips in female apes. Critics claim that without postcranial evidence it is premature to claim that *Sahelanthropus* is bipedal (Su 2013).

Paleoecological data suggest that this *Sahelanthropus* specimen died near a lakeshore and the area was extensively forested.

Orrorin tugenensis

Found in 2000 by a team led by Martin Pickford and Brigitte Senut, Orrorin tugenensis is represented by a collection of fossils that include a minimum of five individuals. Fragments of numerous fossilized body parts were found: jaw, femur, humerus, and finger bones. Many teeth were found, including molars and canines. The binomial reflects where the fossils were found, the Tugen Hills region of Kenya. *Orrorin* means "original man" in the Tugen dialect. Using multiple dating techniques, including paleomagnetism and biochronology, the Tugen Hills fossils are dated to about 6.0 mya.

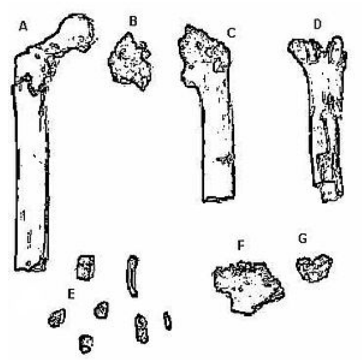

Figure 3.2.2 - *Orrorin tugenensis* fossils

Like *Sahelanthropus*, *Orrorin* has a mix of ape-like and human-like traits. Its teeth are more ape-like so the determination of bipedality is central to attributing the fossils to that of a hominin. The founding research team claims that features of the femur indicate that *Orrorin* was a biped and in the direct line to modern humans. More recent studies suggest that *Orrorin* was in fact a bipedal hominin, but not in the direct line to *Homo* (Richmond and Jungers 2008).

The paleoecological evidence associated with *Orrorin* fossils suggests that the area was a woodland populated with lakes and streams.

Ardipithecus

Two different species of *Ardipithecus* have been identified: ***Ar. kaddaba*** and ***Ar. ramidus***. The two species are differentiated primarily on the C/P3 complex (canine-premolar features), specifically, that A*r. kaddaba's* canines are more primitive than those of *Ar. ramidus*.

Ar. kaddaba is the older of the two species. It is dated to 5.8-5.2 mya. Tim White, Gen Suwa, and Yohannes Haile Selassie discovered *Ar. kaddaba*fossils in the Middle Awash region of Ethiopia. The fossil collection is comprised of fragments of the mandible and teeth, forearm, clavicle, and fourth toe. The shape of the upper canine is more human-like than ape-like in that they are smaller with a more circular crown. Overall, the postcranial fragments are more ape-like; however, the toe bone mentioned previously is similar to the toe bones of *Australopithecus afarensis*, a species that had all the hallmarks of habitual bipedalism. Other researchers claim that a single fourth toe bone does not provide enough evidence to confirm that *Ar. kaddaba* was a bipedal hominin.

Figure 3.2.3 - *Ardipithecus ramidus:* Ardi skeleton

Paleoecological data suggest that *Ar. kaddaba* lived in a "closed, densely-wooded habitat close to permanent water sources (e.g., lakes and/or rivers) with swampy conditions and floodplain grasslands" (Becoming Human c2008).

Tim White is also credited with the discovery of *Ar. ramidus* in Aramis, Ethiopia. Dated to about 4.4 mya, *Ar. ramidus* "represents the oldest species that possesses features unequivocally linked to the hominin lineage. Thus, *Ar. ramidus* is the best evidence discovered thus far for the root of the hominin family tree" (Becoming Human c2008). Paleoanthropologists know more about *Ar. ramidus* than the previously mentioned species as 110 specimens have been unearthed at Aramis.

Postcranially, *Ar. ramidus* is still ape-like; however there are some features that suggest the species could walk bipedally, but it most likely spent time in the trees much like modern chimpanzees. In other words, its mosaic characteristics suggest facultative bipedalism. Features that lead researchers to claim *Ar. ramidus* could walk bipedally include the position of the foramen magnum and features of the spine and ilium.

Early hominins

Australopithecus anamensis

Australopithecus anamensis, meaning "southern ape of the lake," was found by Maeve Leakey and Alan Walker in 1994 in Kanapoi, Kenya. Additional A*u. anamensis* fossils were recovered at Allia Bay, Kenya and several sites in Ethiopia: Asa Issie, Woranso-Mille, and Fejej. Fossil specimens include mandibles, maxilla, teeth, a partial humerus, tibia, manual phalanx, capitate, partial femur, several vertebrae, and a partial temporal bone (Ward et al 2013). Using radioisotopic dating methods on volcanic deposits, *Au. anamensis* dates to 4.1-3.9 mya. The fossil evidence suggests that *Au. anamensis* is ancestral to *Au. afarensis*.

Figure $\mathbf{3.2.4}$ - *Australopithecus anamensis* fossils

Au. anamensis exhibits a mosaic of ape-like and *Homo*-like features. The size and shape of the teeth, especially the lower premolar and upper canine, the u-shaped dental arcade, and the prognathism are some of the ape-like features, while the thickness of the enamel and the breadth of the molars are more like early *Homo*. The single wrist bone is also like *Homo*. Lower limb bones suggest *Au. anamensis* was fully bipedal.

Paleoecological data suggest that *Au. anamensis* lived in forested areas near streams.

Australopithecus afarensis

Discovered by Donald Johanson in 1974 at Hadar, Ethiopia, *Australopithecus afarensis* is arguably the most well know fossil hominin species. It is dated from 3.7-3.0 mya (Scarre 2014). Johanson's discovery in 1974 was, at the time, the most complete hominin fossil. Over 40% of the skeleton was recovered, which allowed the team to fully reconstruct the skeleton. This fossil specimen, named Lucy, coupled with footprints found at Laetoli, Tanzania, in 1978 by Mary Leakey, confirmed that *Au. afarensis* was fully bipedal, albeit not exactly like modern humans. The footprints at Laetoli indicate that *Au. afarensis* had a short stride and a strolling gait. Since the 1970s, hundreds of specimens of Au. afarensis have been found (60 individuals at least from Hadar alone!) in Ethiopia, Kenya, and Tanzania, allowing paleoanthropologists to make "definitive [emphasis original] statements about the locomotor pattern and stature of" (Jurmain 2013: 211) this early hominin.

***Figure* 3.2.5** - Reconstruction of the fossil skeleton of "Lucy" the *Australopithecus afarensis*

Au. afarensis has several primitive, or ape-like, features, including a relatively small brain in comparison to *Homo*, a u-shaped dental arcade, a flat nose, a flattened forehead (referred to as platycephaly) and prognathic face. Its canines, while larger than *Homo*, are smaller than earlier hominins. While its brain was larger than earlier hominins, it is still small in comparison to Homo. There is evidence for sexual dimorphism; *Au. afarensis* males were no taller than 5 feet and females about 3-4 feet, similar in proportion to modern African apes. *Au. afarensis* has a suite of derived traits associated with bipedalism; i.e., bowl-shaped pelvis, s-curve of the vertebral column, and knee anatomy. However, the curvature of the fingers and toes and the proportion of the arms to legs suggest to some researchers that *Au. afarensis*spent some time in the trees.

In 2006, Zeresena Alemsegad announced the discovery of a 3.3 million year old *Au. afarensis* child not 4km from where Lucy was found in 1974. It is not only the oldest juvenile fossil ever found, it is also the most complete hominin fossil found to date. Selam, as the fossil was nicknamed (or Lucy's baby or Dikika's baby), confirmed earlier suggestions that *Au. afarensis* was bipedal, yet spent time in the trees. The shoulder structure with its upward pointing shoulder joints and the bony ridge running along the shoulder blades are like that of apes, which would have facilitated arboreal movement even if they were not as fully capable as chimpanzees at moving in trees.

Paleoecological data indicates that *Au. afarensis* lived in both grassland (savanna) and woodland environments.

Australopithecus africanus

Raymond Dart identified *Australopithecus africanus*, “African southern ape,” in 1924, the first australopith to be recognized. This specimen was a juvenile australopith, nicknamed the Taung baby. Based on the position of foramen magnum, Dart claimed it was a bipedal hominin, but his contemporaries refuted his claim as they thought the brain was too small. The paleoanthropological community did not recognize the Taung baby as a hominin until the 1950s at which time other fossil specimens attributed to *Au. africanus* had been found. *Au. africanus* has only been found in southern Africa at such sites as Makapansgat, Sterkfontein, and Taung.

***Figure* 3.2.6** - *Australopithecus africanus* (Mrs. Ples)

Using primarily biochronological methods since South Africa does not have geologic deposits suitable for other types of dating techniques, it has been dated to 3-2 mya (Scarre 2014). In comparison to *Au. afarensis*, *Au. africanus* has smaller incisors and larger molars; the canines no longer have the pointed, triangular appearance seen in apes and *Au. afarensis*; however, *Au. africanus* still exhibits some prognathism in the face and has a small brain like that of *Au. afarensis*. Postcranially, *Au. africanus* retains some primitive features like those seen in *Au. afarensis*, e.g., shorter arms than legs and hand/feet shape. Its size is also similar to *Au. afarensis*. Another derived feature are the nasal pillars. Nasal pillars are a “buttressing of bone on either side of the nasal opening of the skill on the maxilla,” which may be an adaptation for eating hard foods (Becoming Human c.2008). Other derived traits include a longer, flatter occipital bone and a taller frontal bone, two traits seen in the genus *Homo*. Because of the traits mentioned above, there is general consensus that *Au. africanus* is a direct descendent of *Au. afarensis*. Some paleoanthropologists suggest that *Au. africanus* is the progenitor of *Paranthropus* robustus (see below). Its relationship to *Homo* is less clear.

Australopithecus garhi

Found in Bouri, Ethiopia in 1997 by Behane Asfaw and Tim White, *Australopithecus garhi* is a gracile australopith. “Gracile” refers to the thickness of the bone; in this case it is less robust than its Paranthropus contemporaries. Using radioisotopic and biochronometric dating methods, *Au. garhi* dates to 2.5 mya. Few fossil specimens have been found and those that have are relatively fragmentary. One cranium and other skull fragments were found and serve as the basis of the species identification. The size and shape of its molar teeth suggest to some researchers that *Au. garhi* is related to *Paranthropus aethiopicus* (see below), but its other features, e.g., braincase, face, and other teeth, are more like genus *Homo*. In light of this, some researchers contend it is ancestral to *Homo*.

***Figure* 3.2.7** - *Australopithecus garhi*

Australopithecus sediba

A relative newcomer to the stage, *Australopithecus sediba* was found in 2008 at Malapa Cave, South Africa by Matthew Berger, the 9-year-old-son of the project’s lead paleoanthropologist, Lee Berger. Dating to 1.95-1.75 mya using paleomagnetism, uranium-lead dating, and biochronology, *Au. sediba* has a mosaic of characteristics that suggest it may be transitional from the australopiths to genus *Homo,* hence its name “wellspring or fountain” in the local Lesotho language. However, this claim is controversial as the earliest dates for *Homo* predate *Au. sediba* by about 500,000 years (Becoming Human c2008).

***Figure* 3.2.8** - *Australopithecus sediba*

Au. sediba shares some traits with *Au. africanus*, e.g., cranial capacity, brow ridges, and enlarged tooth cusps (the pointed tops of teeth), causing some to claim the two species are related. Its arm-to-leg proportions are likewise similar to the australopiths. The features that link *Au. sediba* to *Homo* include the pelvis shape, more vertical brain case, smaller cheek bones, and molar shape.

Another controversy recently emerged in 2014 when Ella Been and Yoel Rak presented their spinal cord study (Barras 2014). They claim that the spinal cord features and the jawbones of the two specimens identified by Berger are actually two different species: early *Homo* and an australopith. Additionally, Been and Rak claim the Malapa collection contains the remains of four individuals, not two. Berger disputes this claim that there are two species present. You can read more details about this debate atNew Scientist [optional].

Robust Australopiths

Three robust species of hominins emerged in the Plio-Pleistocene period: *Paranthropus aethiopicus*, *Paranthropus boisei*, and *Paranthropus robustus*. They have morphological features that suggest they were well adapted for eating hard foods that needed grinding, which led to their being identified as “robust.” Their incisors and canines are small, while their premolars and molars are quite large. The zygomatic arch is flared, allowing for larger masticatory muscles that are needed to grind hard foods. This tends to make the face dish-like. A prominent sagittal crest tops the skull, yet another chewing adaptation as it the hard-working temporalis muscle a sturdy bone on which to attach. It has been argued that the robust australopiths were so well adapted that they could not respond quickly enough to changing environmental conditions, which led to their extinction by 1.0 mya. Recently, dental evidence from *P. boisei*suggests that hard foods were not the primary diet of at least *P. boisei*, but were fall back foods, or foods that were ate when preferred foods were not available (Becoming Human c2008).

Note

There is debate over whether the differences mentioned above qualify the robust australopiths to be in a separate genus from the australopithecines. In some anthropological works the genus *Australopithecus* is used. In others, such as this work, *Paranthropus* is used.

Paranthropus aethiopicus

Paranthropus aethiopicus is dated 2.7-2.3 mya. While it was first identified as a species in 1967 by French researchers who found a toothless mandible at Omo, Ethiopia, it was not accepted until 1985 when Alan Walker and Richard Leakey found the “black skull” at Lake Turkana, Kenya. It is called the black skull because during the fossilization process it was stained black by minerals present in the sediment. Other *P. aethiopicus* fossils have been found at Laetoli, Kenya since the 1985 discovery; however, no postcranial material has ever been recovered.

***Figure* 3.2.9** - *Paranthropus aethiopicus*

P. aethiopicus exhibits a powerful jaw, well-developed sagittal crest, and megadont, or extremely large, molars. Its cranial capacity, the joints between the jaw and cranium, and prognathic face are similar to *Au. afarensis*. The prominence of the sagittal crest toward the back of the skull is also similar to *Au. afarensis*. These features are not present in other robust australopiths or *Au. africanus*. These similarities lead some paleoanthropologists to claim *Au. afarensis* is ancestral to *P. aethiopicus*.

P. aethiopicus shares several characteristics with other robust species such as forward positioned zygomatic arches, a dished face (see *P. boisei* reconstruction below), thick palate bones, and large premolars and molars.

Paranthropus boisei

Paranthropus boisei shares several features with *P. aethiopicus*, including a dished face, strong sagittal crest, and large premolars and molars (in fact the molars are about four times as large as modern humans (Smithsonian 2015)). Unlike *P. aethiopicus*, the sagittal crest is positioned towards the front of the skull instead of the back. Other unique features include premolars shaped like molars, the zygomatic arch forms a circular arch, the foramen magnum is short and heart-shaped, and the braincase is large than the other robust australopiths. Little was known about the postcranial structures of *P. boisei* until a 2010/11 discovery of fragments of postcranial remains at Olduvai Gorge, Tanzania. Fragments of the radius, ulna, femur, and tibia support earlier suggestions that *P. boisei* was sexually dimorphic. These postcranial remains indicate that *P. boisei* was “...more ruggedly built—combining terrestrial bipedal locomotion and some arboreal behaviors…it [has] more well-formed forearms muscles that were used for climbing, fine-manipulation and all sorts of behavior” (Sci-News.com 2013).

***Figure* $3.2.10$** - *Paranthropus boisei*

P. boisei was discovered in 1955 at Olduvai Gorge by Mary Leakey. It was not until 1959 that Leakey identified the fossil as a new species and it *Zinjanthropus boisei*, nicknamed “Zinj.” Subsequent discoveries of similar fossils and other robust australopiths resulted in a consensus among researchers that Zinj belonged in the genus *Paranthropus*. *P. boisei* fossils have been found in several East Africa sites, including Peninj, Tanzania, Konso, Ethiopia, and Koobi Fora and West Turkana, both in Kenya. It lived in grasslands, but also forested areas near water sources, between 2.3-1.2 mya, making it a long-lived species. There is no evidence to suggest that *P. boisei* is ancestral to any subsequent hominin.

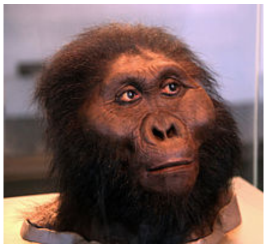

***Figure* $3.2.11$** - *Paranthropus boisei*; model of adult male (Smithsonian Museum of Natural History)

Paranthropus robustus

Paranthropus robustus is the only robust australopith found in southern Africa. First discovered in 1938 by Robert Broom in Kromdraii, South Africa, *P. robustus* fossils were also recovered from Swartkrans and Drimolen, South Africa. Like the other robust species, it has megadont cheek teeth (premolars and molars), large zygomatic arches, dish-shaped face, sagittal crest, and a high degree of sexual dimorphism. Its unique characteristics include a larger brain size than other australopiths and hand morphology suggesting a grip capable of tool use. *P. robustus* is dated 2.0-1.2 mya.

***Figure* $3.2.12$** - *Paranthropus robustus*

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3.3: Homo Genus

The emergence of the genus *Homo* marks the advent of larger brains, the emergence of material culture (at least material culture that survives in the archaeological record), and the eventual colonization of the world outside of Africa. The earliest *Homo* species are contemporaneous with several australopiths: *Au. africanus*, *Au. garhi*, *Au. sediba*, and all of the *Paranthropus* species. Africa was flush with hominins (Figure 3.3.0). There are several trends we see in the evolution of the earliest *Homo* species to ourselves, *Homo sapiens*:

- Rounding of the cranium
- Enlargement and rewiring of the brain
- Smaller faces and teeth
- Decreasing prognathism
- Tallness
- Diversity of cultural traits

As with the overview on early hominins, we will continue taking the lumper approach. Several *Homo* species will not be discussed in detail, but may be mentioned in passing, e.g., *Homo rudolfensis*, *Homo ergaster*, *Homo gautengensis*, *Homo antecessor*, *Homo cepranensis*, *Homo rhodesiensis*, *Homo tsaichangensis*. We will first examine the morphological characteristics of various *Homo* species. Cultural traits will be addressed separately.

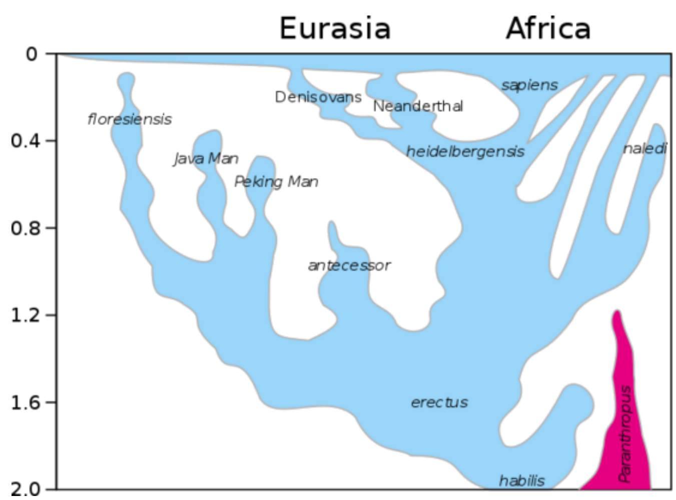

***Figure 3.3.0**: A model of the evolution of the genus Homo over the last 2 million years (vertical axis). The rapid "Out of Africa" expansion of H. sapiens is indicated at the top of the diagram, with admixture indicated with Neanderthals, Denisovans, and unspecified archaic African hominins. Late survival of robust australopithecines (Paranthropus) alongside Homo until 1.2 Mya is indicated in purple.*

Homo habilis

Homo habilis was first discovered by Louis and Mary Leakey at Olduvai Gorge, Tanzania in 1960. Associated with stone tools (Oldowan), the Leakeys named their discover "handy man." *H. habilis* fossils have been found in Tanzania, Kenya, Ethiopia, and South Africa, although there is some debate as to whether the South Africa specimens should be included in the species. Some paleoanthropologist contend that there was another early *Homo* species, *Homo rudolfensis*, which date back to 2.4mya. The *H. rudolfensis* fossils are slightly larger than those of *H. habilis*, leading some researchers to suggest the *H. habilis* exhibited sexual dimorphism and what we are seeing are male and female specimens of *H. habilis*. Others claim the size differences are significant enough to warrant the two species designations (O'Neil c1999-2012). In 2013 a *Homo* mandible was discovered in the Ledi-Geraru research area, Afar, Ethiopia. Dated to 2.8 to 2.75mya, the mandible exhibits an *Australopithecus*-like chin and *Homo*-like teeth (Villmoare et al. 2015). While still early in the research process, this discovery and further research may push back the date of the origin of *Homo* and help to resolve the debate between the *H. rudolfensis* and *H. habilis* fossils. For our purpose, we will consider them all *H. habilis*, making the date range for this hominin 2.4-1.4mya.

***Figure* 3.3.1** - *Homo habilis*

Morphologically, *H. habilis* has a larger brain than the australopiths, about 35% larger (O'Neil c1999-2012). You will recall from the section on trends in human evolution that the brain also began to rewire at this point. *H. erectus* exhibits less prognathism and platycephaly than early hominins. The brow ridge is also smaller. All of these traits together make the face smaller than the australopiths. Postcranially, *H. habilis* exhibit a mix of primitive and derived traits. Primitive traits connecting it to an australopith ancestor are the longer forearms and the size of the finger bones along with how the tendons attach to the wrist bones. The tips of the finger bones are broad like humans. Smaller teeth, a dental arcade in the shape of a parabolic arch, foot morphology, and a more rounded skull complete the human-like traits. Microanalysis of tooth wear indicates that *H. habilis* was omnivorous.

Homo erectus

Based on current fossil data, *Homo erectus* existed between 1.9mya to 25 kya (thousand years ago) (Jurmain 2013). Eugene Dubois found the first *H. erectus*, literally "upright human," fossil in 1891 in Trinil, Java. *H. erectus* fossils have also been found in Africa, China, Europe, and Israel. Based on morphological differences in the cranium, some scientists identify two species, *H. erectus* in Asia and *H. ergaster* in Africa with the African specimens being smaller than the Asian; however, we will use the *H. erectus* designation.

***Figure* 3.3.2** - *Homo erectus*: Turkana Boy

H. erectus is the first hominin to reach modern human height. In 1984, a nearly complete *H. erectus* skeleton was found along the Nariokotome River in northern Kenya. Potassium-argon dating places "Turkana Boy" between 1.64 and 1.33mya. Aging and sexing of the fossil remains indicate that the individual was a male about age eight. He stood about 5'3" tall. If *H. erectus* followed the growth pattern of modern humans then Turkana Boy could have reached 6' as an adult; however recent studies indicate that

Turkana Boy followed the growth pattern of apes, so would have been near his adult height at the time of his death (Jurmain et al. 2013).

The pattern of increased brain size continued with *H. erectus*; its brain is up to 50% larger than its predecessor (O'Neil c1999-2012). This large brain was supported by a diet heavy in meat and other proteins. Its distinguishing characteristics include its sagittal keeling (a thickening of bone that runs from front to back on top of the skull) massive brow ridges (supraorbital tori) and bony prominences on the back of the skull. These prominences give the back of *H. erectus*' skull a pentagon shape from behind. From the side, its skull is football-shaped. Postcranially, *H. erectus*' bones are thicker than *H. habilis*, as were its jaws and face bones, and the proportion of arms to legs is lie that of modern humans, causing some to suggest that its bipedal gait was like ours. The length of its leg bones indicates that *H. erectus* would have been an efficient long-distance runner, allowing them to "run down small and even medium size game animals on the tropical savannas of East Africa" (O'Neil c1999-2012). If so, it is likely that *H. erectus* had much less body hair then its predecessors, as they would have needed to be able to sweat efficiently. Based on studies of human body lice, we know that head lice and pubic hair lice, or crab lice, are separate species. Crab lice are actually more closely related to gorilla hair lice then human head hair lice. The loss of body hair created a barrier between the two species, allowing them both to thrive on humans. DNA studies of the two species indicate that they split 3.0mya, suggesting that humans started to lose their body hair at that time. It is possible that *H. erectus* had little body hair (NOVA 2011).

Scientists generally agree that *H. erectus* was the first hominin to leave Africa. As mentioned previously, fossils have been found in Africa, China, Europe, and Israel. At Dmanisi, Republic of Georgia, fossils were found in strata dated to 1.7mya suggesting that *H. erectus* left Africa soon after it evolved. A recent report (Dembo et al. 2015) posits that *H. habilis* was the first hominin to leave Africa, not *H. erectus*. Should this contention be supported with more data, it can still be argued that *H. erectus* was quite successful in colonizing the Old World, helped, no doubt, by its advanced cultural behaviors.

There is general consensus that *H. erectus* evolved from *H. habilis* and *Homo heidelbergensis* evolved from *H. erectus* in Africa, eventually supplanting *H. erectus* populations in the Old World (Figure $3.3.0$).

Homo heidelbergensis

Some publications, e.g. Larsen 2014, refer to *H. heidelbergensis* as archaic *Homo sapiens*, but for our purposes, we will use the *H. heidelbergensis* designation. Otto Schoetensack found the first *Homo heidelbergensis* fossils in 1907 in Mauer, Germany. Since then *H. heidelbergensis* fossils have been found in Africa, Europe, and Asia. The date range for the species is 800 kya to 350 kya. Primitive traits include its large supraorbital tori, low frontal bone, sagittal keeling, and low frontal bone. Derived traits include separate supraorbital tori over each eye orbit, a more vertical posterior cranial vault, wide parietal bones in relation to the cranial base, and a larger cranial capacity than *H. erectus* (Becoming Human c2008). Additionally, they exhibit sexual dimorphism similar to that of modern humans.

***Figure* $3.3.3$** - *Homo heidelbergensis*

There is regional variation in the morphology of *H. heidelbergensis*. European specimens found at Atapuerca, (Spain), Petralona (Greece), Seinheim (Germany), and Swancombe (England) show that they had compact bodies, which could have been a response to living in the cold climates of the north as it would help to conserve heat. Additionally, the cranium is a mosaic of *H. erectus* traits and derived traits. In Asia, data from sites such as Zhoukoudian, Jinniushan, and Dali (China) show a mix of *H. erectus* and *H. sapiens* traits; the latter includes large cranial capacity and thin braincase walls. African specimens from Kabwe (Zambia), Florisbad (South Africa), Laetoli (Tanzania), and Bodo (Ethiopia) also show a combination of *H. erectus* and *H. sapiens* traits. It shares the massive supraorbital tori and prominent occipital torus with *H. erectus* and thin cranial vault bones, less angulated occipital, and cranial base with *H. sapiens*.

H. heidelbergensis is the common ancestor of *Homo neanderthalensis* in Europe and *Homo sapiens* in Africa.

Homo neanderthalensis

Numerous Neanderthal fossils have been recovered since its discovery in 1856 in the Neander Valley, Germany. While the name of the person who found the first fossil is unknown it was described and named by William King. Neanderthals have been the speculation of scientists and the general public ever since. Some anthropologists classify Neanderthals as a subspecies of *Homo sapiens*, *Homo sapiens neanderthalensis*, while others interpret the morphological differences as significant enough to warrant classifying them as a different species, *Homo neanderthalensis*. In this essay, we will use the latter designation.

***Figure* 3.3.4** - *Homo neanderthalensis*

True Neanderthals first appear in the fossil record about 200 kya, with fossils exhibiting Neanderthal-like characteristics appearing as early as 400 kya. Recent research indicates that Neanderthals went extinct between 41 kya and 39 kya (Higham et al. 2014). Molecular research denotes that some Neanderthal DNA lives on in modern humans, approximately 2% of the DNA of "people who descend from Europeans, Asians, and other non-Africans is Neanderthal" (Callaway 2014). The Neanderthal genes are involved in fighting infections, dealing with ultraviolet radiation (Callaway 2014), and living at high altitudes (Callaway 2015). Neanderthal DNA has recently been linked with depression, obesity, and certain skin disorders, e.g., lesions caused by sun exposure (Callaway 2015).

Neanderthals are the only hominin to originally evolve in a glacial environment, leading to some characteristics adapted for the cold climate. Many scientists contend that the midface prognathism allowed for enlarged sinuses that functioned to warm and add moisture to the cold, dry air before entering the lungs. Small holes below the eye orbits, called the infraorbital foramina, are larger in the European Neanderthals that modern humans, suggesting that the blood vessels were larger, which allowed for more blood flow to the face. This would have helped keep the face warmer. They are relatively short and stocky, males averaging 5' 5" and females 5'1", with shorter appendages, both of which would help to conserve heat by providing less surface area from which to radiate heat. Their leg bones are thick and dense, suggesting that they frequently walked and ran, most likely in food procurement activities. Some postulate that some Neanderthals had pale skin that would have helped increase Vitamin D synthesis by increasing the amount of UV radiation to be absorbed by the body (O'Neil c1999-2014). The width of their body trunks and short tibias fit the predictions for cold weather adaptation as proposed by Christopher Ruff (Larsen 2013). The brain size of Neanderthals may also be related to cold weather. Averaging a cranial capacity between 1300 to 1400 cm3, they have the largest brains of all hominins, including H. sapiens. The size may be associated with increased metabolic efficiency in cold weather, which is similar to modern Inuit peoples today who have a larger brain size than other human populations (Jurmain et al. 2013).

The presence of an occipital bun is one of the characteristics used to identify *H. neanderthalensis* specimens, although it should be noted that this characteristics persists in a small percentage of modern human populations. The occipital bun may have evolved to counterbalance Neanderthal's heavy face when running; it prevents the head from making huge horizontal accelerations (NOVA 2002). The occipital bun also makes the skull elongated in comparison to *H. sapiens*. They had heavy brow ridges like those of *H. heidelbergensis*. Neanderthal skulls recovered from Amud and Tabun in Israel exhibit more *H. sapiens*-like cranial characteristics, including lack of an occipital bun, smaller eye orbits, tall and wide nasal openings, and smaller teeth (Larsen 2014).

Denisovans

In 2010, scientists announced the discovery and DNA analysis of a finger bone and two teeth found in Denisova Cave, Siberia (Reich et al. 2010). The artifacts were recovered from a deposit dated to 50 kya to 30 kya. Data suggest that the remains were from an individual who shared a common origin with Neanderthals, but was not a Neanderthal, nor was it a modern human. The Denisovan individual(s) share 4-6% of its genetic material with modern peoples living in New Guinea, Bougainville Islands, and

China. Further studies (Cooper and Stringer 2013) indicate that the Denisovans crossed Eurasia and interbred with modern humans, but genetically the Denisovans were more closely related to Neanderthals then modern humans (Meyer et al. 2012). While further finds will shed more light on the Denisovans, it is clear that there was more genetic variability during the Pleistocene then previously thought (Larsen 2014), but that gene flow between the various populations had implications for the emergence of modern humans (Pääbo 2015).

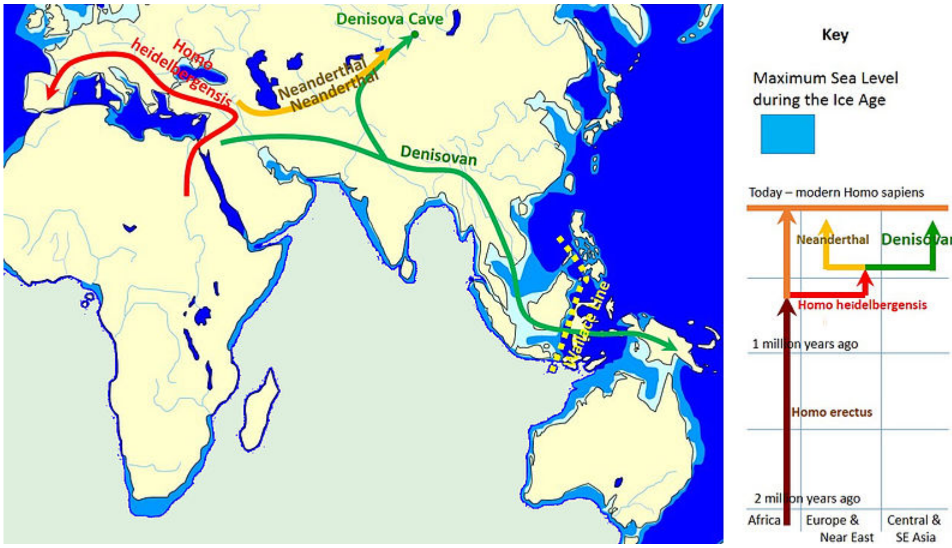

***Figure* 3.3.5** - *Spread and Evolution of Denisovans*

Homo floresiensis

In 2003, Peter Brown and Michael Morwood led a team that discovered unusual fossils in Liang Bua cave, Flores Island, Indonesia. The small stature of the individual led to the naming of a new species, *Homo floresiensis*. Since then twelve individuals have been found ranging in time from 74 kya to 17 kya. *H. floresiensis* had a small brain and stood only about 3.5' tall as an adult. They had receding foreheads, no chins, shrugged-forward shoulders, and large feet relative to their short legs. They share some characteristics with *H. sapiens*, including smaller dentition, separate brow ridges, and a non-prognathic face.

***Figure* 3.3.6** - *Homo floresiensis*

Several hypotheses have been proposed to explain the appearance of *H. floresiensis*. One hypothesis suggests that we are seeing island dwarfism, which is an evolutionary process resulting from long-term isolation on a small island. Limited resources and lack of predators selects for smaller bodied individuals who need fewer resources then large-bodied individuals. Another hypothesis claims that *H. floresiensis*is not a separate species, but *H. sapiens* exhibiting microcephaly or some other developmental deficiency such as hyperthyroid cretinism (Oxnard et al. 2010) because the "…cranial features…are within the modern range of variation seen in living populations from the larger region [of Indonesia]" (Larsen 2014: 409), lending support to the second hypothesis. How *H. floresiensis* fits into the evolutionary picture is unclear based on the current data. An overview of the various hypotheses about its evolutionary relationships in the article, *Homo floresiensis*: Making Sense of the Small-Bodied Hominin Fossils from Flores.

Homo sapiens

At present, only one hominin species inhabits planet Earth, *Homo sapiens*. Morphologically, *H. sapiens* characteristics include the presence of a chin (or mental prominence), a large brain, flat face, rounded or globular cranium, and a continuous, reduced brow ridge. Its bones are gracile in comparison to earlier hominins, although the earliest *H. sapiens* are more robust than modern populations and shows none of the cold weather adaptations of Neanderthals. The more gracile nature lends credence to the hypothesis that modern humans evolved first in Africa. The leaner body proportions are more adaptive to the tropical African environments as there would be more body surface area to radiate heat. DNA evidence also supports an African origin. Modern African populations have more genetic diversity then any other modern human population, inferring that they have been evolving longer (Becoming Human c2008).

Figure $\mathbf{3.3.7}$ - *Homo sapiens*

The oldest *H. sapiens* fossils were found in Africa at Omo Kibish, Ethiopia, dated to 195 kya. *H. sapiens* fossils found at Herto, Ethiopia (160 kya–154 kya), Klasies River Mouth and Border Cave, South Africa (120 kya – 89 kya), Skhūl, Israel (130 kya–100 kya), and Qafzeh, Isreal (120 kya–92 kya), adds further support. Sites in Asia, e.g., Zhoukoudian and Tianyuan in China and Niah Cave, Borneo, Indonesia date to 40 kya or younger and in Europe dating no earlier then 31 kya (Mladeč, Czech Republic). Modern humans made it to Australia by 55 kya; however, no human remains have been found on the continent dating earlier than 30 kya at Lake Mungo. This data lends little support for the Multiregional Hypothesis, a model developed by Milford Wolpoff proposed that modern *H. sapiens* evolved in separate places in the Old World from local archaic *H. sapiens* populations. This model suggested that gene flow between the populations led to the genetic similarity of modern humans. Most anthropologists support the model of an African origin. There are two variants of this model. The Out of Africa model, proposed by Chris Stringer, claims that modern humans arose in Africa and spread to Europe after 50 kya, replacing non-*H. sapiens* population with no gene flow. Fred Smith and Erik Trinkhaus proposed the Assimilation model that also claimed modern human first arose in Africa and spread to Europe and Asia. The primary difference between the Out of Africa and Assimilation models is that the latter does claim gene flow between *H. sapiens* and *H. neanderthalensis*. Taking into account the recent DNA analyses of Neanderthals discussed above, multiple lines of evidence support the Assimilation model.

The case of the disappearing Neanderthals

We know that some Neanderthal genes are in the genome of modern humans, so in essence, some part of the Neanderthals survives today. However, there are no Neanderthals walking around in the modern world. So, what happened to the Neanderthals? Scientists suggest that *H. sapiens* out-competed Neanderthals with their more diverse diet and “sophisticated and cognitive abilities” (Becoming Human c2008). These traits allowed *H. sapiens* to readily adapt to rapidly changing climatic conditions during the Upper Paleolithic.

A recent hypothesis suggests that Neanderthals died out during a period of powerful volcanic activity in western Eurasia. Excavations at Mezmaiskaya Cave in the Caucasus Mountains in southern Russia have recovered a plethora of Neanderthal bones, stone tools, and remains of prey animals. The Neanderthal remains and artifacts appear in strata above a layer of volcanic ash and below a second layer of volcanic ash. No Neanderthal bones or artifacts have been found above the second level, suggesting that Neanderthals no longer occupied the area. Both of the ash layers contain levels of pollen associated with cooler, drier climates. “The ash layers correspond chronologically to what is known as the Campanian Ignimbrite super-eruption, which occurred around 40,000 years ago in modern day Italy, and a smaller eruption thought to have occurred around the same time in the Caucasus Mountains” (University of Chicago Press Journals 2010). The ensuing volcanic winter caused a dramatic climate shift that led to the demise of the Neanderthals. This data correlates with Higham et al.’s (2014) research that claims Neanderthals went extinct between 41 kya and 39 kya.

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3.4: Material Culture

The earliest evidence of material culture is in the form of stone tools found on sites dated to 2.4 millions years. This does not mean that early hominins did not use tools. New finds from Dikika, Ethiopia in the Afar region, indicate that *A. afarensis* used stone tools to extract marrow from bones 3.4 million years ago. What this study does not show is whether *A. afarensis* was making tools or using a found rock.

Harmand et al. (2015) published that they had found 3.3 million-year-old (myo) stone tools at Lomekwi 3, West Turkana, Kenya, which they propose calling Lomekwian as the tools predate Oldowan tools (see below) by 700,000 years. What is particuarly interesting is that the oldest *Homo* fossils found in West Turkana are 2.34 myo. Kenyanthropus platyops (not covered in the overview of early hominins, but you can learn about it at Becoming Human) is the only hominin known from the area at that time, although *Au. afarensis* is known from 3.39mya. Questions remain as to which hominin left behind the assemblage (an assemblage is a group of artifacts found together at a specific site) of 149 artifacts, including flake fragments, worked cobbles, and cores, and how it compares with Oldowan tools. As this is such a recent discovery, it is not covered in any more detail on this page.

Osteodontokeratic Culture

Paleoanthropologists have long been interested in the cultural aspects of hominins. Not all of the tool industries identified in the past stood the test of time. The osteodontokeratic tool culture was the earliest tool industry to be described, but was later discredited. In 1949, Raymond Dart, who discovered *A. africanus*, recorded numerous broken animal and hominin bones, horns and teeth at Makapansgat Cave, South Africa. The bones were broken and gnawed and many showed puncture marks. Dart interpreted this find as evidence that hominins used bone, teeth and horn (osteo-donto-keratic) as weapons, not only for hunting but against one another. From this interpretation sprang the idea that early hominins were violent killer-apes, an idea that has remained in the popular zeitgeist to this day.

Years later, C.K. Brain, working at Swartskrans, South Africa, found a similar artifact assemblage. Brain found that about 40% of the hominin fossil assemblage was comprised of young robust australopiths, many of which looked similar to the bones fossils that Dart had found at Makapansgat--they were broken, gnawed and had puncture marks. After a careful taphonomic study, Brain developed the Leopard Hypothesis. He found that the puncture marks were consistent with the width of leopard canines. He concluded that the robust australopiths were hunted. The reason that there were so many young australopiths is that they were more vulnerable, not having the same skills as adult australopiths. He also noted that many of the bones had cut marks over tooth marks, indicating that an animal had gnawed the bones and then a hominin, probably *Homo hablis*, which was also found at the site, scavenged the australopith bones. Brain's work effectively debunked Dart's osteodontokeratic proposal.

Oldowan Tool Industry

The oldest stone tool assemblage is the Oldowan tool industry (at least it is the oldest until the field comes to a consensus about Lomekwian tools). First identified at Olduvai Gorge, Tanzania by Louis and Mary Leakey, Oldowan tools are stone pebble tools manufactured using a hard percussion technique. This technique involves striking two stones together to knock off a flake or create an edge on a piece of stone. While this seems like a simple technique, to make one of these tools, the individual needs to be able to understand how the stone will break when struck. The presence of Oldowan tools is an indication of changing cognitive abilities.

Figure 3.4.1 *- Olduwan flake tool*

Originally, paleoanthropologists thought that the hammerstone was the primary tool used, but microwear analysis, a methodology whereby stone tools are examined under a microscope and the use wear patterns compared to use wear patterns established through experimental archaeology, indicates that the flake tools were the primary tool. Oldowan tools were used for cutting, chopping and scraping.

Louis Leakey believed that the Oldowan tools were evidence that *Homo hablis*, the fossil hominin found associated with the tools at Olduvai Gorge, hunted, especially since numerous animal fossils were found at the site. However, the mere presence of stone tools and animal fossils does not confirm hunting behavior. In the early 1980s, Rob Blumenschine conducted a year-long study on the Serengeti and in riparian (river banks) habitats. Blumenschine observed around 250 feedings by both predatory and scavenger carnivores such as lions, cheetahs, hyenas, and vultures. What he noticed that was when a predator ate, they would eat the meatiest parts of the body, leaving behind primarily limb bones. He suggested that if hominins were hunting that the artifact assemblage should contain those animal bones with the most meat. If hominins were scavenging then limb bones would dominate the fossil animal bone assemblage. Additionally, he noted that if hominins hunted then cut marks from tools would underlie animal tooth marks and vice versus if they were scavenging.

***Figure* $3.4.2$** - *Olduwan chopper*

Armed with this information, the Olduvai Gorge material was reexamined. Several new points came to light: 1) the damage on the bones was most similar to that left by carnivore activity, 2) the percentage of limb bones in the artifact assemblage met the expectations of scavenging behavior, and 3) the cut marks overlay teeth marks. It was clear at this point that *Homo hablis* was not hunting but scavenging. While conducting his research, Blumenschine had used Oldowan tools to scavenge a carcass. He found that in about 10 minutes, it was possible to extract enough meat and bone to meet about 60% of the estimated daily caloric intake (approximately 1500 calories). Blumenschine demonstrated that it was an easy feat to scare off other scavengers and even some predators in order to gain access to the carcass. As a subsistence strategy, scavenging does have some advantages:

- it is less dangerous as the scavenger does not have to risk themselves for the kill
- it is quicker as the scavenger can simply follow the roar of the lion or look for vultures circling overhead
- there is less energy expenditure for the reasons listed above and the short amount of time it would take to butcher the remaining carcass using stone tools

The first definitive evidence of hunting is from Schöningen, Germany in the form of wooden spears dated to 400,000 years. The artifacts were identified as spears because they have similar morphology to modern javelins, e.g., the balance point is 1/3 the way from the spear point. The spears are about 7 feet long with sharpened points and were found with the remains of butchered horses.

Until recently, one of the long running debates has centered on who was the first tool user. With the recent announcement by the Dikika Research Project, the nature of that debate may change from who was the first user to who was the first maker. The previously oldest tools came from Gona, Ethiopia dated to 2.4 million years ago. As these tools were not found associated with any hominin fossils, paleoanthropologists debated who made the tools. The time frame puts several hominins in play: *Au. garhi*, *P. robustus*, *H, rudolfensis*, and *H. habilis*. Studies show that *P. robustus* had the hand morphology for making tools, but many do not think that the species had the cognitive abilities. Plus, no *P. robustus* fossils have been found with stone tools. The same goes for *Au. garhi*. All researchers agree that *Homo* was making and using tools. Again, the recently reported finds from Lomekwi 3 may end up demonstrating that an early australopith was the first tool maker.

Figure 3.4.3 - *Acheulean Handaxes*

Acheulean Tool Industry

One thing we see with tool technologies is that as time passes the tools become more and more sophisticated. About 1.9 million years ago, *Homo erectus* invented a new sophisticated technology for making stone tools, which started with the hard percussion technique, but then employed a soft hammer technique to get more refined and sharper edges. This new tool industry is called the Acheulean.

The Acheulean tool industry, first found at St. Acheul, France, is characterized by bifacial tools. This means that the stone is worked on both sides. This tool industry is a marked step in the cognitive abilities of hominins because the tool has to be conceptualized prior to manufacturing. Dozens of flakes have to be removed precisely in order to maintain the symmetry of the tool and keep the edges straight. The signature tool of the Acheulean tool industry is the tear-drop shaped handaxe. Often referred to as the Swiss Army knife of the Pleistocene, the handaxe was an all-purpose tool used for a multitude of activities including digging, sawing, and cutting.

Mousterian Tool Industry

Neanderthals took the next step in the evolution of stone tools by making tools for specialized tasks. Named after a cave site in Le Moustier, France, these flake tools developed out of a manufacturing technique called the Levallois. This technique first arose with the Acheulean and is characterized by preparing the core of raw material from which flakes can be struck and then worked. Sharper tools with a finer edge are produced using this technique. Neanderthals shaped these flakes into tools like scrapers, blades, and projectile points, specifically spear points. In fact, at Neanderthal caves sites in the Middle East, there are a higher percentage of spear points found than at neighboring Homo sapiens sites. Mousterian tools are a technological advance, taking a high degree of conceptualization and knowledge of the properties of the stone. On average, it takes about 200 blows to make one flake tool.

Figure 3.4.4 - *Levallois points, Mousterian Tool Industry*

Upper Paleolithic Tool Industries

The Upper Paleolithic of Europe begins 45,000 years ago and ushers in further advances in tool technology. Not only are there a wider variety of tools made, but new materials are used, including bone and antler. Several regional types of tool industries emerge in the Upper Paleolithic. The first is the Aurignacian, which is characterized by blade tools. A blade tool is a tool that is at least twice as long as it is wide. The benefit of blade tool technology is that blades can be easily knocked off a prepared core and then made into a wide range of tools, e.g., projectile points, drills, needles, scrapers, burins. By 31,000 years ago, the Aurignacian is widespread throughout Europe, allowing archaeologists to trace the movement of modern *Homo sapiens*.

Figure 3.4.5 *- Aurignacian Backed Knives (Wellcome M0011849)*

The Aurignacian tool industry disappears from the archaeological by 29,000 years ago. It is replaced by the Gravettian tool industry, which is found at European sites until around 21,000 years ago. This tool industry is characterized by small blades and denticulate (serrated) knives. The Gravettian also has projectile points with blunting (steep backing) that can be hafted onto a shaft. The small size of some of the projectile points leads some archaeologists to surmise that the bow and arrow was invented during the Gravettian, although the first definitive evidence of arrows comes from Stellmoor, Germany (10,500 years ago). It does appear that the atlatl, or spearthrower, was invented during this time frame. This is an important advance as it allowed a hunter to throw farther and with more force, making hunting the megafauna of the period a little safer.

Figure 3.4.6 *- Gravettian tools (Fleche Font Robert 231.4 (2))*

The Gravettian is followed by the Solutrean and the Magdelenian tool industries. the Solutrean tool industry is characterized by bifacial, leaf-shaped projectile points. As far as stone tools go, the Solutrean points are some of the best made points of the Upper Paleolithic. The technology flourished from

Figure 3.4.7 *- Solutrean Point*

around 21,000 to 16,000 years ago, but then disappears for thousands of years until a similar manufacturing process appears in North America during the Clovis period. to explain this, some archaeologists propose that there was a migration of peoples from the Iberian Peninsula to North America in the late Pleistocene who carried the technology with them; however, other there is little other evidence to support this contention. It is probable that the manufacturing techniques was rediscovered by North America's early inhabitants.

One of the reasons that Solutrean points were finely made was because the stone was heat treated before it was worked. Heat treatment means that the stone was placed in a fire for a period of time, making it possible to make pressure flaking more precise. Heat treating was also a hallmark of the Magdelenian tool industry, 16,000-11,000 years ago. Bone and antler tools flourish during the Magdelenian. Harpoons appear in the archaeological record, with true barbed harpoons showing up around 13,000 years ago.

***Figure* 3.4.8** - *Magdalenian Barbed Harpoons*

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