UNSW AUSTRALIA | Medical Sciences
Medicine

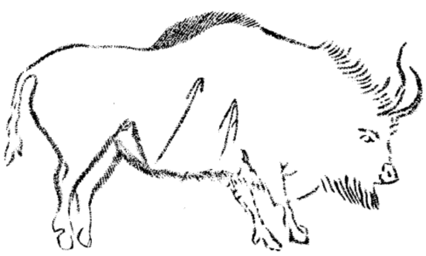
Evolution of Human Structure

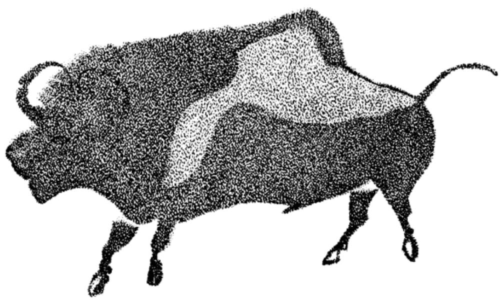
ANAT2521

Course Outline

Summer session 2017

January 3 to February 3





Course Authority:

Professor Ken Ashwell

CRICOS Provider Code 00098G

Please read this outline in conjunction with the following pages on the Medical Sciences website:

- Advice for Students
- Learning Resources

(or see "STUDENTS" tab at medicalsciences.med.unsw.edu.au)

Course authority: Prof. Ken Ashwell (k.ashwell@unsw.edu.au, 9385 2482),
Department of Anatomy, School of Medical Science, Room 261, Wallace Wurth

Lectures: **Wallace Wurth LG02**
Practical Classes: **Wallace Wurth 101 (Gross Anatomy Laboratory)**
Tutorials: **Wallace Wurth 101 (Gross Anatomy Laboratory)**.

IMPORTANT NOTES

- Students must wear enclosed shoes (i.e. no thongs or sandals) in the **Gross Anatomy Laboratory**.
- No eating, drinking or smoking in the **Gross Anatomy Laboratory**.
- Mobile phones must be switched off during lectures and classes.

COURSE AIMS

The aims of this course are to:

1. Provide the student with an understanding of the major biological (physical and evolutionary) attributes of non-human primates and humans.
2. Assist the student to develop a deeper appreciation of the place of humans in the natural world and their relationship to other primates.
3. Provide the student with some knowledge and skills from the field of biological anthropology.
4. Help the student to appreciate the importance and relevance of the study of human origins for an understanding of modern human structure, development and disease.

STUDENT LEARNING OUTCOMES

Students should complete the course knowing (among other things):

1. Some basics of primate and human anatomy, especially of the skeleton, muscles and brain.
2. Anatomical features of the order primata and of major groups of primates.
3. The elements of evolutionary biology and the evidence for human evolution.
4. The broad patterns of evolution for the primates and humans, including major evolutionary trends.
5. The basis for human physical variation across the world and its effect on human diet and disease.
6. The evolutionary basis of modern human structure, with particular reference to the upper and lower limb, brain, birth canal and vocal apparatus.

The University of NSW has developed a list of graduate attributes (see https://medicalsciences.med.unsw.edu.au/students/undergraduate/advice-students). This course and the required assessments will assist the student to develop skills in all of these areas.

ASSESSMENT

one laboratory project assignment, two spot tests, final theory exam

- The laboratory project assessment is worth 20% of the final mark and will be assessed by the tutor. Students will be assessed on: a) the laboratory project and its written report; and b) the oral presentation. Each of these components will have equal weighting (i.e. 10% for the laboratory project & written report and 10% for the oral presentation) in determining the final mark for the paired tasks.
- The two spot tests will each be worth 20% of the final mark. The first spot test will be held at approximately 50% of the course duration and the second at course end. Each will cover the preceding half of the practical classes. Spot tests are held in 101 (Gross Anatomy Lab) of the Wallace Wurth Building.
- The final theory examination is worth 40% of the final mark and will be assessed by the course authority. The 2 hour examination on Friday 3 February 2017 will include 40 multiple choice questions and 3 short essay questions.

RESOURCES

- The course will not require any special library resources. Students will be accessing eJournals to prepare their project reports/oral presentations.

- All practical classes, tutorials and spot-tests will take place in the Gross Anatomy Laboratory (101) of the Department of Anatomy, School of Medical Sciences. All models and specimens required for the course are already available in the collections of the Department of Anatomy.

- Adaptive tutorials will be provided for the students to reinforce concepts introduced during lectures and practical classes. These have been developed by the course authority using Moodle and the SmartSparrow platform.

PREREQUISITES

The course has been given a level 2 identifier, but can be taken at any level, even level 1. There are no prerequisites for the course because all necessary knowledge (e.g. elementary genetics and principles of evolution) is included within the course structure. This has been done to maximize the accessibility of the course for students with non-scientific backgrounds.

Lecture and Practical/Tutorial Schedule

WEEK 1		
Day 1	**Tuesday 3rd January (4 to 5 hours) – lectures in WW LG02**	
10-11	Lecture 1	Introduction to Primate Biology (KA)
11-12	Lecture 2	Elements of Genetics (CL)
12-1	Lecture 3	Diversity and Evolution (CL)
2-3	Lecture 4	Ethics of Human Remains and Forensic Anthropology (CL)
3-3.30	Lecture 4 continued	Interpreting Human Bones (CL)
Day 2	**Wednesday 4th January (5 hours) – lectures in WW LG02**	
10-11	Lecture 5	Principles of Paleoanthropological Techniques (KA)
11-1	Practical 1	Primate Musculoskeletal Anatomy (KA)
2-3	Lecture 6	The Origin and Early Evolution of Primates (KA)
3-4	Film	Ape and Human Behaviour (KA)
Day 3	**Thursday 5th January (5 hours) – lectures in WW LG02**	
10-11	Lecture 7	Early Hominins (KA)
11-12	Lecture 8	*Homo ergaster* and *Homo erectus* (KA)
12-1	Films	Portrayals of Human Ancestors (KA)
2-3	Lecture 9	Archaic *Homo sapiens* (KA)
3-4	Tutorial 1	Group Orientation and Choosing of Project Topics (KA)
WEEK 2		
Day 4	**Monday 9th January (5 hours) – lectures in WW LG02**	
10-11	Lecture 10	Modern *Homo sapiens* (KA)
11-1	Practical 2	Cranial Anatomy of Australopithecines and Early Humans (KA)
2-3	Lecture 11	Humans in Australia (CL)
3-4	Lecture 12	Humans in the Americas (KA)
Day 5	**Tuesday 10th January (5 hours) – lectures in WW LG02**	
10-11	Lecture 13	Evolution of Human Behaviour (KA)
11-12	Lecture 14	Origin and Mechanics of Bipedalism (CL)
1-3	Practical 3	The Human Lower Limb and Bipedal Locomotion (CL)
3-4	Lecture 15	Human Sexuality and the Problems of Human Childbirth (CL)
Day 6	**Wednesday 11th January (5 hours) – lectures in WW LG02**	

10-12	Practical 4	Human Childbirth (CL)
1-2	Lecture 16	The Comparative Anatomy and Function of the Hand (CL)
2-4	Practical 5	The Human Hand and Tool Use (CL)
WEEK 3		
Day 7	**Monday 16th January (5 hours) – lectures in WW LG03**	
10-11	Spot test 1 (based on practical classes 1 to 4)(KA)	
11-12	Lecture 17	The Hominin Brain (KA)
1-3	Practical 6	The Human Brain (KA)
3-4	Lecture 18	Language, Speech and the Human Face (lecture/film)(KA)
The remainder of week 3 is allowed for laboratory project work.		
WEEK 4		
Day 8	**Monday 23rd January (5 hours) – lectures in WW LG02**	
10-12	Practical 7	The Human Face and the Functional Anatomy of Language (KA)
12-1	Lecture 19	Variation and Adaptation of Modern Humans (CL)
2-3	Lecture 20	Changing Patterns of Disease during Human History (KA) Food and Diet (CL)
3-4	Lecture 21	Syphilis, Tuberculosis and HIV/AIDS (KA)
Day 9	**Tuesday 24th January (2 hours) – lectures in WW LG02**	
10-11	Spot Test 2	Spot test 2 (based on practical classes 5 to 7)(KA)
11-12	Lecture 22	Malaria and Human Evolution (CL)
Day 10	**Friday 27th January (up to 4 hours)**	
10-2	Tutorial 2/3	Presentation of Laboratory Projects (KA)
Day 11	**Friday 3rd February (2 hours) – examination in WW LG03**	
9.45-12.00	Final examination (KA)	

KA – Prof Ken Ashwell

CL – Dr Carol Lazer

Lecture 1 Introduction to primate biology

Specific Objectives:
1. To be able to list the key characteristics of primates.
2. To know the main groups of living primates.
3. To be able to explain the key features of primate ecology.
4. To be able to summarize the main threats to the biodiversity of primates.

The key characteristics of primates
These are set out in detail in the class notes for practical 1. Primates are, of course, mammals, which means that they possess body hair, milk (mammary) glands and maintain relatively high body temperature by internal metabolic activity (endothermy). Many of the features that characterize primates are actually 'generalized' features. In other words these mammals have not developed a specialized form in response to evolutionary pressures as have horses or dolphins, but have retained many of the features of the early mammals. This has also meant that primates have been able to evolve in a number of different directions, which explains the great diversity seen among living primates. This is readily seen in the primate upper limb, which has retained some bones that have been lost in other mammals (e.g. the clavicle or collar bone). Primates have a generalized limb structure, which allows them to engage in a range of locomotor activities (e.g. walking on the ground on four limbs, or quadrupedalism, as seen in baboons, or swinging through trees beneath branches, brachiating or arm-swinging, as seen in gibbons). Other important features include a tendency towards an upright body posture, flattened nails (in some, but not all primates), binocular vision, colour vision, grasping hand (some with opposable thumbs or big toes), a general lack of dietary specialization, enlarged brain, a prolonged period of dependency of the infant on the mother and a tendency to live in social groups. Several of these features (binocular vision, grasping hand, vertical posture) are excellent adaptations to life in the trees leading to an **arboreal hypothesis** for primate origins. On the other hand, it has also been noted that binocular vision would have been of great benefit if early primates stalked and captured fast-moving insect prey using vision (**visual predation hypothesis**). The a**ngiosperm radiation hypothesis** proposes that flowering plants provided nectar, seeds and fruit for primates.

Primate teeth are generalized in form, meaning that these animals can eat many different types of food (e.g. fruit, leaves, insects, birds, amphibians and occasionally other mammals). Primates from the Old World (Africa, Europe and Asia) have 2 incisors, 1 canine, 2 premolars and 3 molars on each side of each dental arch. This is known as the **dental formula** and is seen in humans as well as Old World monkeys and apes. New World monkeys have three premolars, whereas the strepsirhines (prosimians) have varying dental formulae.

Most primates are active by day (**diurnal**) whereas the strepsirhines tend to be active by night (**nocturnal**). Primates have shifted from olfactory dependence (as seen for many other terrestrial mammals, e.g. dogs, rats) to visual dependence with colour vision. The ability to detect colour is beneficial in assessing the ripeness of fruit and in detecting insect prey against foliage (see below).

The main groups of living primates

Primates are usually divided into two suborders: **Strepsirhini** (strepsirhines, including lemurs, galagos and lorises) and **Haplorhini** (haplorhines, including tarsiers, monkeys, apes and humans). The haplorhines have enclosed orbits (eye sockets), enlarged brains and fused frontal bones and mandibles. Within the

Haplorhini there is a subdivision into three groups: Superfamily **Ceboidea**, containing new world monkeys, **Cercopithecoidea** containing Old World monkeys, and **Hominoidea** including **apes** (**gibbons, orangutans, gorillas, chimpanzees and bonobos)** and humans.

We shall review the main points of the different primate types in turn:

A) Prosimians

- Most similar of all primates to the early mammalian ancestor.
- Include lemurs (Madagascar) and lorises (Africa, India, SE Asia).
- Pronounced reliance on olfaction – reflected in the moist fleshy pad (rhinarium) at the end of the nose.
- More laterally placed eyes than other primates.
- Different uterine structure from other primates.
- Dental comb specialization of the lower incisors and canines.
- Grooming claw on second toe.

B) Tarsiers

- All live in southeast Asian islands.
- Possess both retained ancestral traits (grooming claw and unfused mandible) and advanced traits (absence of rhinarium and dental comb).
- Large eyes dominating the face.
- Lower limbs adapted for leaping.
- Believed to occupy an evolutionary position between prosimians like the lemurs, and haplorhines like the monkeys and apes.

C) New World Monkeys

- Found in central and south America.
- Almost exclusively arboreal.
- Broad, widely flaring noses with outward facing nostrils (platyrrhine – flat-nosed).
- Include four families: Atelidae – howlers and spider monkeys; Callitrichidae - marmosets and tamarins; Cebidae – capuchins; Pithecidae – sakis.
- 3 premolars in each dental quadrant instead of 2 as in Old World monkeys.

D) Old World Monkeys

- Found in Africa, Asia, India.
- Most are quadrupedal and primarily arboreal.
- Noses are downward facing (catarrhine).
- Females of some species exhibit pronounced cyclical changes in the appearance of the external genitalia (associated with estrus).
- Sexual dimorphism (differences in size between genders) is typical of some terrestrial species and is particularly pronounced in baboons.

E) Hominoids

- 3 families (**Hylobatidae** - gibbons and siamangs; **Pongidae** – orangutans, gorillas, bonobos and chimpanzees; **Hominidae** – humans).
- usually larger than monkeys.
- no tail, shorter trunk than monkeys.
- more complex brain and behaviour than monkeys.
- increased infant dependency.

Interestingly, chimpanzees, bonobos (pygmy chimpanzees) and humans share more genetic similarity than do zebras and horses, or goats and sheep. On this basis it would be appropriate to group humans and chimpanzees within the same family and perhaps the same genus (*Homo*). Humans have 46 (i.e. 23 pairs of) chromosomes, while chimpanzees have 48 (i.e. 24 pairs of). The banding pattern of human chromosome 2 corresponds to those of two much smaller chimpanzee chromosomes (chromosomes 12 and 13). This finding has led to speculation that in an ancestral hominin (human), these two chromosomes fused to produce what became human chromosome 2.

Primate chromosomes, proteins and DNA

Relationships between primates may be revealed by analysis of biochemical and cytogenetic features. These include:

- Karyotyping – the analysis of chromosome shape, size, number and banding patterns.
- Amino acid sequencing – e.g. of blood proteins such as hemoglobin. The more distantly related the primate, the more amino acid substitutions in a given protein.
- DNA hybridisation – testing for differences and similarities between DNA sequences from different primates. Evolutionary similarities/differences are calculated from the number of mismatched base pairs along a hybrid DNA sequence from two primates.
- DNA sequencing – involves determining directly the sequence of nucleotides along a strand of DNA. This data is already available for humans as part of the Human Genome Project, but is not yet available for all primates.

Primate ecology

Most primates are herbivores, existing on a diet of leaves and/or fruit. Some strepsirhines eat insects and the tarsiers are exclusively carnivorous, living on insects, lizards, frogs and other small animals. Fruit eating primates (**frugivores**) must be able to assess when fruit is ripe (colour vision) and cope with the seasonal availability of their food. Leaf eating primates (**folivores**) must cope with the poor nutrient and calorie supply in their diet. Folivores prefer the youngest leaves and shoots because these have the highest ratio of nutrients to indigestible fibre. Plants also produce toxic compounds (tannins, phenols and alkaloids) in their leaves to discourage attacks by folivores. Baboons, chimpanzees and humans supplement their diet with the flesh of other animals.

The diet of a primate greatly influences its anatomy and physiology. Folivores often have large gastrointestinal tracts (e.g. the pot belly of gorillas), sometimes with specialized stomachs for fermentation of the cellulose in plant food. Insectivorous primates tend to be small, because insect eating is more costly in time and energy for large primates, who tend towards folivory.

All mammals live in defined regions called **home ranges**, which must contain all the resources needed by a primate group (water, food, shelter, mates). That part of the home range used most intensively is the **core area**.

Primate conservation

Many primates live in habitats that are under threat from human activities. There are three reasons for the decline in primate numbers worldwide:

- Habitat depletion
- Hunting
- Live capture for export or local trade

Lectures 2 & 3 Elements of genetics / Diversity and evolution

These lectures introduce concepts and terminologies (marked in bold) that are used in many of the subsequent lectures and practical classes throughout the course. The detailed notes are intended as reference and general background for non-biologists.

It should not be necessary to take additional notes so you can relax and concentrate on the images and concepts. What you need to know is included in the lecture notes.

Lecture 2 Elements of genetics

Specific Objectives

1. To describe the location, structure and function of the genetic material (DNA), including the processes of the molecule copying itself (replication) and reading of the genetic code to make proteins (transcription and translation).
2. To list types of coding errors (mutations) with examples of their effects.
3. To know basic terminology and patterns of inheritance of simple genetic traits.

Introduction

Evolution is a process that changes the form of **populations** (groups of breeding individuals) over successive generations. To understand the mechanics of this process it is necessary to know some basic molecular and general genetics concepts and terminology.

All organisms (plants, animals, bacteria, etc) are made of **cells**, which contain their own organs (organelles), are able to copy themselves, and can produce the molecules necessary for survival. An important group of molecules, called **proteins**, perform numerous functions including: structural *(fibres, like collagen, elastin, keratin, etc)*, chemical *(enzymes that act as catalysts for chemical reactions)*, communication *(hormones)*, transport *(carriers for other molecules, like oxygen and fats)*, buffers *(to maintain constant blood pH)*, etc. All proteins are constructed according to coded instructions stored in the genetic material, which is another important group of molecules, called **nucleic acids**. There are two forms of nucleic acid, DNA and RNA.

Every organism inherits the specific details to make all its proteins. This comprises the **genetic code** or **genome**. All organisms which share common codes for their proteins form distinct species, whereas slight variations in parts of this code make all individuals unique. How these variations are inherited in a population forms the basis of the process known as **evolution**.

The genetic material

The genetic code is carried on long molecules of DNA, known as **chromosomes**, which are found in the nucleus of cells. The molecular structure of DNA and RNA explains both how the code is conserved and how it is read.

The DNA molecule is made up of atoms of carbon, hydrogen, oxygen, nitrogen, phosphorus, etc, to form two spiral strands called a **double helix**. Each strand is a chain of alternating sugar and phosphate molecules linked together by pairs of molecules, called **bases**. A unit of sugar, phosphate and base is called a **nucleotide**. Each long chain in a nucleic acid comprises a string of joined nucleotides. The cross-links between the strands are made by four bases which link in specific pairs: Adenine always pairs with Thymine (two hydrogen bonds A=T) and Cytosine always pairs with Guanine (three hydrogen bonds C≡G). **DNA** (deoxyribonucleic acid) is a double helix (two stranded) with deoxyribose as the sugar molecule. **RNA** (ribonucleic acid) is a single helix (one stranded) with ribose as the sugar molecule and the base Uracil instead of Thymine (A=U).

The genetic material is conserved, in that exact copies are made automatically (**replication**) each time a cell divides. An enzyme splits the hydrogen bonds between the bases separating the two strands of each DNA molecule. Nucleotides present in the nucleus match up with the unpaired bases like jigsaw pieces to re-establish the complementary strands using each split original as a template.

The order of the bases along the DNA molecule is the **genetic code**. DNA holds the whole code in the nucleus but a piece of code copied to an RNA molecule (**transcription**) can be carried from the nucleus to ribosomes in the cytoplasm, where the sequence of bases in the RNA will be "read" to assemble a specific protein molecule (**translation**).

To achieve this, a section of the DNA of a chromosome is split open by an enzyme, as in replication, and a string of code (**gene**) on one strand is copied, or transcribed, as RNA to carry the **complement** of that code from the nucleus into the cell. This messenger RNA (**mRNA**) attaches to ribosomes, the sites where it is decoded, or translated, and protein construction occurs.

Proteins are made of strings of a group of chemicals called **amino acids**. There are 20 different amino acids and their sequence determines the properties of the protein, such as how the molecule will fold and interact with other molecules. The final shape of the protein is critical to its proper function.

Floating in the fluid cytoplasm of the cell are specially folded RNA molecules that carry amino acids to the ribosomes for protein assembly. This transfer RNA (**tRNA**) has three unpaired bases at one end of the molecule and the particular amino acid coded by the complement of that sequence at the other end. Hence, the genetic code is read in "words" of three "letters" (triplets) from an "alphabet" of four bases. A code of doublets would allow 4x4 or 16 combinations, which is not enough for 20 amino acids. A code of triplets enables 4x4x4 or 64 combinations to provide coding redundancy as well as start and stop codes. Each **triplet** (three bases) on the mRNA is called a **codon** and the complimentary set of three bases on the tRNA is called the **anticodon**. Only one anticodon will pair with the next codon on the mRNA at the binding site on the ribosome, so only the tRNA carrying the next correct amino acid will be brought alongside the growing amino acid chain to link with it. As the chain gets longer each disconnected tRNA molecule is released and recycled to collect its specific replacement amino acid in the cytoplasm. This process produces the primary structure of a protein, the amino acid sequence. It will then fold into simple helix or pleated sheet sections to form the secondary structure, which will further fold into a complex 3-D shape to form the tertiary structure. Some proteins form a quaternary structure where two or more tertiary protein chains bind to each other. An example is haemoglobin in red blood cells which is made of four molecules, two α chains and two β chains.

If a change occurs in the genetic code, often as an error in replication, it will result in misreading of the codons with a subsequent change to the final protein. This is called a **mutation**. Typical errors include: deletion (loss of a base), addition (an extra base), or substitution (replacement of the correct base by another). One or more mutations may change the ability of a protein to function correctly. This might have no obvious effect, or cause an illness if it occurs in body cells (benign tumour or cancer), or an inherited condition if it occurs in sex cells (abnormality or genetic disease).

The influence of mutation can be quite varied depending on the protein affected. A change to a structural protein can affect its function, such as a single base substitution in the β chain of haemoglobin to produce sickle cell anaemia. Abnormal enzymes interfere with metabolic pathways. Inheritance of different ineffective enzymes causes very different illnesses, even when they belong to the same biochemical pathway. A defect in any enzyme along the path, such as the conversion of food from the diet to the pigment molecule, melanin, will cause the process to stop at different points. For example, if the enzyme that converts phenylalanine (an amino acid from protein in our food) into tyrosine (another amino acid) is defective, then phenylalanine will build up to toxic levels in a baby and cause brain damage with mental retardation, a disease known as phenylketonuria. If a different enzyme that converts a metabolic product of tyrosine to melanin is defective, the individual will lack pigment, a condition known as albinism. Note that sufferers of phenylketonuria have the pale appearance of an albino, since the metabolic pathway has been blocked further back than the chemical product needed by the other normal enzyme to produce melanin.

These concepts and processes form the underlying mechanics of genetics and evolution.

Inheritance of characteristics

During most of the time in the cell cycle the individual, long molecules of DNA (**chromosomes**) cannot be seen (interphase) but they become highly coiled and shortened during cell division (**mitosis**), which occurs in several stages (prophase, metaphase, anaphase, telophase) and are easily seen under the microscope. They are often shown in photographs as stained chromosomes spread out from the metaphase stage of cell division. With special stains the chromosomes show consistent patterns of light and dark bands. The photographed images of these chromosomes are arranged and numbered in order by size and the position of the constriction (**centromere**) to produce a **karyotype**. All the chromosomes in a nucleus form an individual's karyotype, which is typical for the species. In humans there are 46 chromosomes, being two sets of 23 chromosomes, one from each parent. Manipulation of the physical properties of DNA in the laboratory shows that chimpanzees and humans share around 98% of their DNA (the number varies slightly with sources) but some of it appears to be distributed differently. Human chromosome 2 corresponds in banding pattern to the two smaller chimp chromosomes 12 and 13. This would explain why humans have 46 chromosomes and chimps have 48, suggesting fusion in the hominid line of two chromosomes that remained separate in the ape line (or vice versa).

The base sequence on each chromosome codes for many different proteins and the code for any one protein is called a **gene**. The gene for each protein will occupy the same location (**locus**) on the same chromosome in all individuals. Since chromosomes occur in duplicate there are two copies of the same gene for each protein. Each copy is not always identical with slight code variations (from mutation), called **alleles**. An individual can carry two copies of the same allele (**homozygous**) or two different alleles (**heterozygous**) inherited from their parents. When two different alleles occur together the outward appearance will usually be of only one of them and that one is called **dominant**. The other is called **recessive**. The alleles carried (**genotype**) produce the outward appearance (**phenotype**). As a simplified example, genes for the pigment molecules of eye colour code for pigment proteins that can vary in size in the iris of the eye. The small molecules scatter the light to give a blue colour, while large molecules absorb light to give a brown colour. By convention the variants (**traits**) are identified by a letter from the alphabet with the dominant trait capitalized. Brown eyes (large molecules) are dominant to blue eyes (small molecules), so the genotypes homozygous brown (BB), homozygous blue (bb) and heterozygous Bb will have the phenotypes of brown eyes, blue eyes and brown eyes respectively.

Knowing this allows understanding of the patterns of inheritance. A blue eyed parent must be bb and a brown eyed parent could be BB or Bb. If a child has blue eyes (bb), the brown eyed parent must be Bb and the probability of blue eyes is 0.5 or 50% for each child. If two brown eyed parents have a blue eyed child, then they must both be heterozygous (Bb) with a 0.25 or 25% probability for each child having blue eyes.

Lecture 3 Diversity and evolution

Specific Objectives

1. To list several sources of variation and diversity.
2. To describe the principles of mitochondrial and Y chromosome inheritance.
3. To be able to discuss key concepts of population change and the process of evolution.

Generating Diversity

The process of DNA replication occurs whenever the cells of the body divide (**mitosis**) or when the sex cells of the body are formed (**meiosis**). In mitosis each cell division produces two identical daughter cells, each with the same DNA. In meiosis the genetic material is rearranged and the DNA content halved through two cell divisions. The two sets of chromosomes (maternal and paternal chromosomes) are randomly separated (**independent assortment**) with some exchange of complementary genetic material between maternal and paternal chromosomes (**recombination**). In meiosis four sex cells are produced, where each has half the chromosome number and none are genetically identical. This ensures that genetic variability is maintained between the generations independently of new mutations. Note that the **purpose of sex** is to contribute a genetic remix from each parent to produce new genetically related but unique individuals.

This can be illustrated by another simplified example using two genes, eye colour and hair colour. Hair works in the same manner as eye colour with the allele for dark hair (D) being dominant to fair hair (d). A blue eyed / dark haired parent (bbDd) and a brown eyed / fair haired parent (Bbdd) could have the following children: blue eyes / dark hair (bbDd), brown eyes / fair hair (Bbdd), both looking like one of their parents, or blue eyes / fair hair (bbdd), brown eyes / dark hair (bBDd), both unlike either parent with new phenotypes.

Some genes have more than two alleles but only a maximum of two will occur in any individual. For a gene with two alleles only two phenotypes are possible. For a gene with three alleles more variations are available. One of the red blood cell groups is coded by a gene with three alleles (I^A, I^B, i), two being equally dominant (codominant) and one recessive, to produce four phenotypes (A, B, AB, O). In the case of tissue types, several genes are involved (with 4-5 routinely tested), and each has multiple alleles (6-12, or more). It is easy to see why it is so difficult to find compatible tissue matched donors for transplants when so many available combinations make each individual effectively unique. Inherited variation can be even more complex than this. Some phenotypes result from the interaction of multiple genes and environmental influences, known as **multifactorial inheritance**. Two examples are height and intelligence, where the combined genetic potential of many genes can be influenced by such factors as nutrition, childhood illness, education, etc. This makes the allocation of characteristics to racial types very tenuous.

The female line (mitochondrial Eve) and the male line (Y chromosome)

There are two kinds of DNA in a cell. Most is found in the nucleus (**nuclear DNA**) but a small amount is present in an organelle called the mitochondrion (**mitochondrial DNA**). Mitochondria are the site of cellular respiration and are thought to have been bacteria that now live exclusively inside cells. They have maintained their own DNA for self-replication and to produce the enzymes necessary for the conversion of sugar and oxygen to energy.

Sex in most species is determined by two special chromosomes, a medium sized X and a small Y chromosome. In humans, the 46 chromosomes comprise 22 pairs of chromosomes common to both sexes (**autosomes**) and one pair of **sex chromosomes**. Females have two X chromosomes while males have an X and a Y. The egg will carry one of the two maternal X's while the sperm can carry either an X or a Y, so it is the father that determines the sex of the offspring.

The egg is a gigantic cell, while the sperm is tiny in comparison. All the cytoplasm and organelles in the cells of our bodies originated from the cytoplasm of the egg, whereas the only contribution of the sperm is half the nuclear DNA. This means that all our mitochondria and its DNA came from our mothers. Similarly, the Y chromosome, common to all men, could only be carried by the sperm and so all Y chromosomes in men came from their fathers.

Stable DNA avoids the processes that generate diversity and changes very little over time. It includes mitochondrial DNA that does not undergo meiosis, or genes unique to the Y chromosome that do not take part in recombination during meiosis. Studies of the diversity of genes of stable DNA are used to compare the relative ages of populations. Older, ancestral populations accumulate more genetic changes, through non-lethal mutations, than recently separated populations. If all mitochondrial DNA is inherited through the female line we can theoretically "look back" to the original mother of the line, the so called **mitochondrial Eve**. The same principle applies through the male line by looking at the **Y chromosome segment** that is unique and does not pair with the X chromosome.

How evolution works

Physical form is strongly related to function and both are influenced by environmental conditions. Evolution, often referred to as **Darwinian evolution**, is a process that acts on the form and function of individuals in the short term and changes populations in the long term. Genetic variation within populations (**gene pool**) provides the basic material through which evolution acts by changing gene (allele) frequencies. In this context the populations are called **species**, which are true breeding groups that cannot successfully interbreed with other groups. Any isolated breeding group, such as separated colonies of a species, will be subject to local evolutionary pressures. If such an isolated group diverges sufficiently from the original it becomes a new species (**speciation**).

More individuals are born than will survive. In a varied population individuals will be removed from the gene pool through predation, illness, competition for breeding sites or mates, non-viable offspring, etc. Associated with environmental change, a few individuals may fare better than the rest to leave many offspring to the next generation. This process where an individual's ability to breed is affected by the environment is called **natural selection**.

Mutation is often cited in popular fiction as the source of variation which drives evolution. This is not the case as most mutations are disadvantageous (*naked neck chicken*) or lethal (*sickle cell anemia*), a few are relatively benign (*albino*), and almost none will bestow advantage in the current environment. It is **sexual reproduction** with the independent assortment and recombination of meiosis that rearranges the allele combinations and creates much of the variation in a population.

Even so, potentially fatal phenotypes do turn up in populations. Dead or disadvantaged individuals will not breed and pass their genes to the next generation but these mutations, although rare, always occur to recreate alleles that are being lost. The population frequency of a lethal allele will be close to the mutation rate. Recessive deleterious or lethal alleles are often masked by the normal dominant alleles. The frequency of hidden alleles for abnormal traits in a population is called the **genetic load**. With a change in the environment, a normally deleterious or benign allele may confer advantage, so this load is a potentially important source of hidden variation. For example, drug resistant properties in the chemical makeup of a few bacteria in a population may be of no value, or even a slight disadvantage, till the appropriate drug is encountered in the environment. Then the resistant bacteria will have a selective advantage (they will not be dead) and so produce most of the offspring of the next generation to become a drug resistant strain.

The concept of fitness is another Darwinian idea that has been corrupted by popular fiction. **Fitness** does not refer to the physical strength or aggression of an individual but to how many offspring that individual leaves to grow up and reproduce. Only those individuals well suited to the environment will successfully produce offspring and pass their genes (allele combinations) to the next generation. For example, rare white rabbits in woodland are easily seen by predators and so have a low fitness (no offspring) compared to the other well camouflaged, brown rabbits. A change to the environment where snow becomes predominant would confer a much higher fitness to any white rabbits that are now better camouflaged than the brown rabbits. With increased reproductive success the allele frequency for white rabbits, and subsequently the number of white rabbits, will increase in the population.

It should be noted that evolution can never "design" a perfect or novel organism. New structures cannot be created but existing structures can be modified to fit a new function (**divergence**). For example, the basic body structure is four limbs, so wings can develop from modified forelimbs, such as a bird or bat, but another pair of limbs cannot be produced from nothing to form a four legged and winged dragon. Change can only build on what is already present (**homology**) to give the best fit to the environment at the time with the best **compromise**.

If the environmental challenges are the same the solutions will be similar, leading to **convergent evolution**. Two examples are adaptations to exploit air and sea. More than one group of plants and animals have independently developed flight with membranous extensions common to winged seeds, flying squirrels and gliding possums, and unrelated modifications of the forelimb to become wings in flying prehistoric reptiles, birds and bats. The penguin, seal and whale have undergone similar changes for a life dependent on swimming with conversion of limbs to paddles and rudders and a body shape similar to fish. These structures look similar because they are the best responses to the common needs imposed for staying airborne or moving efficiently underwater. Another less extreme example is the tendency for many species to develop large, heavy jaws and teeth associated with a high proportion of tough vegetable fibre in the diet.

Populations are shaped by their environment but there is no such thing as the perfect population. Environments will always change forcing population change, a process known as **dynamic equilibrium**. A documented example for a species of moth in England illustrates this principle well, where colour change occurred in moth populations in response to environmental change. A population of light coloured moths had evolved to camouflage against pale lichens on the bark of trees. Black moths would occasionally occur but these had low fitness as they were easily seen by birds and eaten. The industrial revolution covered the trees with black soot. The light moths, now easy to see, had reduced fitness while the fitness of the rare, dark moths increased. Over a several generations the population frequency of the allele for dark colour increased, to produce a population of dark moths. Occasional light moths would continue to occur with low fitness. Conservation efforts eventually forced industries to clean up with a drop in the level of pollution. With less soot the pale lichens were able to re-colonise the tree trunks. The dark moths were now at a selective disadvantage, while the rare light moths survived to produce many young and so change the gene frequency again; this time to favour the allele for light colour. Over several generations, the moth population changed back to its original pale colour with the occurrence of occasional dark moths.

Highly specialised species can be too closely tied to their environment. It can spell disaster if the environment changes too radically or too rapidly, as it takes generations to effect population change. For example, koalas eat leaves from a limited range of trees and risk extinction wherever their forests become threatened. The possum has a very flexible diet and easily adapts to new environments, like the urban landscape that replaces their native vegetation. It is no accident that a generalised animal, like the shrew, was the forebear of the primates as it formed an uncomplicated “blank slate” for physical adaptations to exploit life in the tree tops.

There is **no direction** in evolution. There is no such thing as an evolutionary hierarchy to a superior form over an inherently primitive form. This notion is another legacy of popular culture which suggests that humans are the pinnacle of primate evolution. It is often projected further to predict a future, mentally superior being with a small body and very big head, much like most popular representations of aliens. Evolution cannot produce a final form, only a current form with the best fit to the current environmental conditions.

It can be argued that modern humans are the only exception to the evolutionary process as they tend to modify their environment to suit themselves rather than be modified by their environment. For example, humans have rapidly spread into a wide variety of climatic extremes without modification of form. Any other species would need generations of time to develop major adaptations to a new environment, such as thick fur to protect from extreme cold. However, there are many examples of human variation that has been influenced by evolutionary pressures.

Lecture 4 Ethics of human remains and forensic anthropology

Specific Objectives:

1. To be able to demonstrate an understanding of the concepts of ethics and morals in relation to the issues associated with the study of ancient human remains.
2. To appreciate that these are dynamic and that there are no correct answers – each case must be considered in conjunction with the people that identify as stakeholders.
3. To know the main types of information that we can learn from forensic investigation of human skeletal remains.
4. To understand the constraints of forensic identification of human skeletal remains.

What are ethics?

Ethics has been defined as the science of morals or moral principles. They involve systematic reflection on moral issues. Morals are concerned with correct conduct. They are based on a perception of what is right and wrong. The problem lies with the determination of what actually is right and wrong. Attitudes vary between cultures and can change over time. It is also possible for a cultural group to alter accepted opinions over a short time span. In addition, there may be a number of opinions within one cultural group as to what is right and wrong for a particular issue. This is certainly the case when it comes to the study of human remains from archaeological contexts. **Because of this problem there are no correct answers when it comes to determining what should be done. The best course of action can only be established on a case-by-case basis.**

There was a tradition of collecting, studying and displaying human remains, generally without consent, in western society that continued well into the 20th century. A number of studies were associated with establishing the racial supremacy of those who were examining collections of human material. From the latter half of the 20th century, there was increasing pressure by certain groups of people to have their remains returned, often for reburial. As a result of successful lobbying, laws have been enacted to facilitate this process, such as the Native American Graves Protection and Repatriation Act, which was approved by President Bush in 1990.

In addition to legal requirements, a number of institutions which house collections of skeletal remains of Indigenous people have responded to pressure from Indigenous communities by developing policies. For example, the University of Sydney has a Repatriation Policy, which means that there is consultation with each appropriate community and if they choose to have their ancestor's bones repatriated, the bones are returned with due ceremony. When the human skeletal remains are returned, the community is also presented with a plain English summary of the results of the investigations that have been made on these bones.

There has been some discussion in recent years about whether it is appropriate to exhume the remains of ancient individuals, like Egyptian mummies, whose remains were deposited in tombs with the expectation that they would spend eternity in their final resting place.

It is important for appropriate communities to be consulted if remains are to be excavated. Some archaeologists have developed good community relationships with Indigenous people, which has lead to co-operative research programs, involving the excavation and analysis of human remains.

Codes of Ethics and Guidelines

To help scholars address the difficult issues associated with the ethics of dealing with human remains, sets of guidelines and codes of ethics have been established. Generally, to abide by a code of ethics, researchers must make a commitment to the development of a research plan and consult with appropriate groups or individuals who claim some association, either cultural or genetic (i.e. the stakeholders), to the material under investigation. If the consultation is successful, scholars should work with the sanction of stakeholders. The results of any research should be made public within a reasonable time and reports in plain or traditional languages should be presented to stakeholders.

Many associations in different countries have developed codes of ethics. Examples include the Code of Ethics of the Australian Archaeological Association, Archaeological Institute of America Code of Ethics, American Board of Forensic Examiners Code of Ethical Conduct, National Association for the Practice of Anthropology Ethical Guidelines and the World Archaeological Congress Code of Ethics.

Originally, codes of ethics mostly involved consideration of Indigenous people but there has been a shift in attitude over the last twenty years. There is now much more interest in dealing with the remains of other cultures, including the remains of modern western individuals in a more sensitive manner. There is no doubt that there has been a flow on effect from the need to address the wishes of traditional communities. This has resulted in the development of a series of guidelines for dealing with European remains and cemeteries. It is notable that Australia has been one of the leaders in this field. In 2005, English Heritage produced guidelines for the reburial of old Christian bones.

These issues were not initially considered relevant for the fossilised remains of possible human ancestors but there is increasing interest in who can claim a direct link with this material. Some scholars have argued that all modern humans are stakeholders and that the knowledge that can be gained from studying these remains is more important than the concerns of individual communities.

Display of Human remains

Some groups of people, like Indigenous Australian people, consider that it is highly inappropriate to display the remains of their ancestors to the public. There has been much discussion in recent years about whether the remains of ancient people who have been removed from tombs, should be displayed as they were clearly meant to spend eternity in their resting places.

Bodies that have been recovered from peat bogs have been displayed in museums. In the case of the so-called Tollund Man, only his head was conserved and displayed. New technology is being developed to enable holographic displays of bog people.

Similar to the use of holograms, is the use of casting techniques to create replicas of human remains, which can be left in situ. This means that the original material can be studied and stored appropriately.

It is important to note that not all cultures consider that the display of human remains is offensive. There is a long tradition of displaying human anatomical images in Europe, often in an extremely theatrical manner. The major work of the sixteenth century anatomist, Andreas Vesalius of Brussels, *De Humani Corpus Fabrica*, includes detailed woodcuts of humans divesting themselves of layers of their anatomy, often within the setting of a romantic landscape. The exhibitions of plastinated bodies devised by Gunther von Hagens, while considered highly offensive by some people, clearly operate within this tradition. It is possible that some of the public outrage about Von Hagen's exhibitions of posed humans reflects a shift in attitude.

There is a tradition dating back to medieval times of public exhibition of human remains for religious purposes. Natural mummification of deceased individuals who had been placed in crypts, for example, was considered to be the result of divine intervention, as a failure to putrefy was seen as suspension of the laws of nature, and such bodies were usually displayed. Similarly, monks and laic supporters of the Capuchin monastery at Palermo, who were either naturally or artificially mummified between the sixteenth and turn of the twentieth centuries, are on view in subterranean chambers of the building. Sometimes bodies have been exhibited to emphasise views about the Resurrection and the separation of body and soul, like the disarticulated remains of approximately 4000 Capuchin brothers and other individuals who died between 1528 and 1870. These bones have been used to form elaborate patterns, such as a clock made from vertebrae and other skeletal elements, that decorate the crypt of Santa Maria della Concezione in Rome.

Forensic anthropology

Most skeletons from archaeological contexts are not complete but it is still possible to gain information from them by applying modern forensic techniques to attempt to establish sex, age-at-death, pathology, lifestyle indicators and an estimate of height. Some bones are more useful indicators than others, for example the adult pelvis is the most useful bone to determine the sex of an individual, though most other adult bones also provide information about sex. It is extremely difficult to determine sex from a juvenile skeleton.

Conversely, it is much easier to determine age-at-death from juvenile bones and teeth as they are growing and developing. Once these processes are completed, the only changes that occur are degenerative, and these vary greatly between individuals.

A number of scholars are overly optimistic about what information can be revealed from a skeletal study, such as hair, eye colour and the exact age-at-death of adults. Human skeletal remains are also unlikely to provide accurate information about social status from unknown populations, most occupations, weight and the number of pregnancies that have come to term.

It is very important to appreciate that the techniques for skeletal identification are based on studies of modern populations, which cannot necessarily be extrapolated onto ancient unknown populations with any degree of certainty.

Film: The ape: that human being

Lecture 5 Principles of paleoanthropological techniques

Specific Objectives:

1. To be able to indicate the range of subdisciplines of paleoanthropology.
2. To be able to define the terms palynology, paleoecology, taphonomy, primary context and secondary context of paleoanthropological and archaeological traces.
3. To define the difference between relative, calibrated relative and absolute (chronometric) dating methods.
4. To describe modern dating methods and indicate the advantages and disadvantages of each.
5. To define experimental archeology and the methods used to test hypotheses concerning tool use.

Subdisciplines in paleoanthropology

Modern paleoanthropology (the study of ancient humans) depends on the coordinated efforts of scientists from many different disciplines. These include geologists, who engage in the initial surveys of potential fossil sites; vertebrate paleontologists to identify animal remains and assist in finding potentially fossil bearing beds, archaeologists to search for hominin cultural traces (i.e. artifacts like stone tools), physical anthropologists to study and classify fossil human remains, geophysicists and geochemists to assist in dating of finds or the strata in which they are found, and palynologists to identify pollens and help build up a picture of the climate of the area during the time when deposits were laid down.

Paleoecology and the context of paleoanthropological finds

Study of the types of animal present at a site (**vertebrate paleontology**) along with data concerning the pervading vegetation as revealed by **palynology** (the study of pollens) will help build up a picture of the local **paleoecological** setting (ancient environment). Another important area of study is **taphonomy**, the study of how bones and other materials come to be buried in the sediment as fossils. This depends on the actions of streams, the preservation characteristics of bones, the activities of carnivores and the geological processes of sedimentation. This is particularly important because paleoanthropologists need to understand the depositional history of the site they are studying, i.e. whether remains were laid down and fossilized without disruption (i.e. **primary context**) or whether there has been movement of whole or part of the remains due to the actions of streams, herds of herbivores or carnivores for example (**secondary context**). Paleoanthropologists need to be cautious about drawing too many conclusions concerning culture from material found in a secondary context, since predators may have greatly modified the remains, giving a false impression of hominin behaviour. A good example of this is the early ideas by Raymond Dart concerning **osteodentatokeratic culture** of southern australopithecines: the association of hominin remains with the teeth and bones of other animals does not prove that the hominins used such as tools. Such associations could be the result of predator activity or deposition by water.

Dating methods

Obviously accurate dating is essential to the interpretation of human remains. There are three broad groups of dating methods: **relative dating techniques**, **calibrated relative dating techniques** and **absolute (chronometric) dating**.

Relative dating methods tell the paleoanthropologists that a particular find is younger or older than another find. It does not give any indication of the actual number of years involved. A good example is **stratigraphic dating**, which depends on the geological law of superposition. This states that a lower stratum or layer of geological sediment must be older than an overlying stratum. Problems with stratigraphic dating include shifting of strata by volcanic and river activity and mountain building. Also, the stratigraphic record may not be complete in any one region and it is difficult to know how long a period of time was required for a given stratum to accumulate. Nevertheless, with careful correlation of stratigraphic records from different regions, often achieved with the aid of the fossils found in each (**biostratigraphy**), this method provides a useful tool for paleoanthropologists. Another relative dating technique is **fluorine analysis**, which depends on the progressive incorporation of fluorine into bones during the fossilization process – the longer a bone is in the earth the more fluorine it accumulates. This technique is only useful for comparing the relative ages of bones found in the same context, but proved very useful for demonstrating that the Piltdown remains were a hoax. In that case the jaw (later shown to be that of an orangutan!) was found to be younger than the (human) cranium. Another type of relative dating technique is **dendrochronology**, which uses tree ring correlation to derive a sequence of yearly rings that can be used to determine the age of a tree trunk. The latter is mainly applicable for recent human prehistory (e.g. archaeology of southwestern USA).

Calibrated relative dating techniques include regular or somewhat regular processes that can be calibrated to a chronological scale if certain conditions are known. A good example is paleomagnetism. Reversals in **paleomagnetism** (i.e. changes in the direction or polarity of the earth's magnetic field) occur at irregular but known times and are useful for cross-checking radioactive decay based techniques (see below). Paleomagnetic methods depend on the fact that the periodic reversals in the polarity of the earth's magnetic field are imprinted upon rock deposited at that time and can be assessed in the laboratory. Note that paleomagnetism would be of minimal use on its own because polarities reverse at irregular intervals and for prolonged periods and because only two geomagnetic states are possible (normal or reversed).

Chronometric dating methods often depend on radioactive decay of isotopes. Depending on the isotope used, it is possible to date items ranging in age from the beginning of the earth to as recent as a few hundred years ago. Uranium 238 decays with a half-life of 4.5 billion years to form lead. This allows geologists to date the age of formation of the earth. **Potassium 40** decays to produce Argon 40 with a half-life of 1.25 billion years and is useful in dating materials in the 1 to 5 million year range (the period of appearance of most human ancestors). A related variant is the **Argon 40/Argon 39** technique which allows analysis of small crystals and is more accurate than standard K/Ar dating. The types of rocks that provide the best samples for these techniques are those that have been heated to very high temperatures (i.e. by volcanic activity). The well-known **Carbon 14** technique (half-life of 5,730 years) is actually only useful to date material from 1,000 years to 75,000, with a substantial decline in accuracy over 40,000 years.

Another important dating technique is **fission track dating**, which depends on counting the number of Uranium 238 nuclei that have spontaneously fissioned as revealed by the number of tracks left in a mineral or natural glass sample. This technique is applicable to dates covering human evolution (up to 5 mya) as well as relatively recent (a few thousand years). Note that dating techniques need to be cross-checked against each other to maximize accuracy and that dates for fossils should always be expressed with an error margin of $\pm$ one standard deviation.

Chronometric techniques that do not rely on decay of radioactive isotopes within the specimen include the **electron trap techniques**. These techniques rely on measuring the number of electrons in a specimen that have been dislodged by external radiation. These dislodged electrons become trapped in defects within crystals in the specimen, so only crystalline materials can be dated. Electron trap techniques include thermoluminescence, optically stimulated luminescence and electron spin resonance. **Thermoluminescence** (TL) measures the number of trapped electrons from the amount of light given off by the specimen during heating. It is particularly applicable to objects that have had the crystal electron traps emptied by heating during the past (e.g. pottery or rocks around a fireplace) and has been used for objects up to 100,000 years old. **Optically stimulated luminescence** (OSL) dates materials whose electron traps were emptied by bleaching with sunlight and therefore dates the time at which something was buried. The object is exposed to light of a particular wavelength and the resulting luminescence measured. This method is useful for dating Australian rock paintings covered by wasp mud. **Electron spin resonance** (ESR) is used most for dating tooth enamel. Trapped electrons resonate as they absorb microwaves and the amount of resonance is proportional to the number of trapped electrons.

Experimental archeology

It is also possible to gain useful information of ancient human cultures by trying to reproduce the techniques for manufacturing hominin artifacts. This applies in particular to stone tool technology. Don't underestimate the difficulty of producing stone tools. Modern stone tool-makers (**knappers**) take many years to develop the appropriate techniques for making some of the more delicate stone tools. Once stone tools have been reproduced we can proceed to use experimental archeology techniques to test hypotheses about the uses to which those stone tools were put. By comparing microwear patterns on modern experimental tools with that seen on ancient artifacts, it is possible to determine whether the ancient tools were used on wood, bone, meat or hide, or for cutting or scraping. Scanning electron microscopy can be used to detect phytoliths – non-organic residues from plant material on tool edges, as indicators of the purposes to which the tools were put.

Bone analysis

Ancient bone can be analyzed for information of the effects of water, carnivores, butchering by hominins, or weathering processes. Stone tools leave very characteristic marks on bone when they are used to butcher carcasses or deflesh skulls as part of funeral rites.

Lecture 6 The origins and early evolution of primates

Specific objectives:

1. To be able to define the terms homology and homoplasy and indicate the principles of cladistic analysis.
2. To be able to summarize key events and fossils in primate evolution through the Eocene, Oligocene and Miocene.
3. To be able to summarize macroevolutionary processes, defining the terms adaptive radiation and speciation and indicating the differences between gradualist and punctuated equilibrium models of macroevolution.
4. To be able to define the terms genus and species as they are applied to living and extinct primates.

Introduction

The field of biology that specializes in delineating the rules of classification of living things is **taxonomy**. Classification has traditionally been based on structure (Linnaeus system) although this has some limitations. More recently protein structure and genetic similarity have become useful tools in classification. Structures that are shared by species on the basis of descent from a common ancestor are called **homologies** (e.g. the pentadactyl plan of terrestrial vertebrates). On the other hand, some animals develop superficially similar structures through response to a similar lifestyle or environment (e.g. birds and insects both have wings). These similarities, based on independent functional adaptation and not on shared evolutionary descent, are called **analogies**. The process that leads to the development of analogies is termed **homoplasy**. In the case of primates, the similarities between New and Old World monkeys would be a case of homoplasy, in view of the long period of enforced separation of these two primate types thanks to the expansion of the Atlantic Ocean.

Interpreting evolutionary relationships

There are two approaches to the interpretation of evolutionary relationships. **Evolutionary systematics** is the more traditional and depends on the tracing of ancestors and descendants through time by analysis of homologous characters. **Cladistics** depends on analysis of particular types of homologous structures, i.e. those that can be said to be **derived** or **modified**. **Primitive** or ancestral traits are those that are shared because of a common remote ancestor and have not changed subsequently. Traditional systematics illustrates the hypothesized evolutionary relationships between animals using a **phylogeny** or **phylogenetic tree**. Cladistic analysis shows relationships using a **cladogram**. The key difference between the two is that the phylogenetic tree incorporates time whereas a cladogram (strictly speaking) does not incorporate the time dimension and makes no attempt to determine ancestor/descendant relationships.

Mammalian radiation after the end of the Cretaceous

Many paleontologists maintain that we owe the mammalian diversity of our modern world to a catastrophic event 65 million years ago (K-T boundary event), when an enormous comet or asteroid about 10 km across struck the earth in the region of the modern Yucatan peninsula of Central America. (Note that alternative views emphasize vulcanism and gradual environmental deterioration). The resulting global winter caused the extinction of the large (non-avian) dinosaur species as well as many marine reptiles (end-Cretaceous extinction) and allowed mammals to radiate into large bodied forms. Note that dinosaurs did not become extinct, because avian dinosaurs survived and are now extremely successful as modern birds (12,000 species compared to only 5,000 species of mammals).

Most of mammalian radiation and evolution into the many forms we see today has taken place during the Cenozoic, which has lasted for about 65 million years. The Cenozoic consists of the Tertiary period (63 million years duration) and the Quaternary (about 1.8 million years duration). We have already seen that primates share the basic placental mammalian features of viviparity (live birth), heterodont dentition (different teeth types for different purposes), large brain and endothermy.

Key events in primate evolution

Many primate fossils have been identified from deposits ranging in age back to 55 million years ago (mya). It was originally thought that early primates were derived from a group of mammals known as the **Plesiadapids** (plesiadapiforms) of the Paleocene (65 to 55 mya), but this view has been questioned. Plesiadapiforms are now seen as being closely linked to the ancestral primates, but are believed to have already diverged in Paleocene times. Plesiadapiforms had small brains, rodent like incisors, and a prognathic (projecting jaw) face. They lacked a postorbital bar and had small orbits located on the side of the face. *Purgatorius* is the earliest known fossil of this type and dates back to the very earliest Cenozoic. The divergence of strepsirhine and haplorhine lineages is believed to have occurred by 58 mya.

The first truly convincing primates belong to the Eocene (55 to 34 mya - mainly from North America and Europe). This was a time of high global temperatures, when forests rich in insects and flowering plants, key food sources for early primates, covered most of the globe. These early primates exhibit the full suite of anatomical features that characterize modern primates. The precise relationships between these different ancestral primates and modern groups remains uncertain, certainly these ancestral forms (**Adapoids** and **Omomyoids**) were extinct by the end of the Eocene. The adapoids are believed to be early strepsirhines (before the divergence of lorises from lemurs), whereas the omomyoids are early haplorhines (before the divergence of tarsiers from higher primates), but note that this is controversial. Adapoids probably focused on eating leaves and relied on their sense of smell, whereas omomyoids began to exploit fruit and insects and relied more on vision. During the Eocene, North America was still joined to Europe, thereby allowing movements of primates between the two.

The Oligocene (34 to 23 mya) was a period when Old World anthropoids diversified as revealed by finds from the Fayum region of Egypt. The global climate cooled and dried at the end of the Eocene and many forest-adapted groups became extinct (an event known as the *Grande Coupure*). By the early Oligocene, the Americas and the Old World were well separated, so the finds in North Africa probably represent a distinctly Old World lineage. One important fossil is ***Aegyptopithecus*** (about 32 mya) from Fayum in Egypt, which is believed to be ancestral to both apes and Old World monkeys. *Aegyptopithecus* is thought to have been a short-limbed, slow moving arboreal quadruped. Another genus from the region is ***Apidium*** – small squirrel-sized primates, which led an arboreal quadrupedal existence and may lie near the divergence of New and Old World primates. On the basis of dental similarities, some scientists believe that South American primates are derived from Apidium and reached the isolated continent of South America by rafting across the Atlantic on vegetation cast adrift during storms. The available fossil and molecular evidence suggests that the divergence of anthropoids from other Old World primates occurred after this time (i.e. around 25 mya).

In more recent times (the Miocene - 23 to 5 mya) there were many types of advanced primates in the old world (e.g. ***Proconsul***, ***Dryopithecus*** and ***Sivapithecus***). All of these later fossils are of large-bodied hominoids, that is, more akin to the lineages of orangutans, gorillas, chimpanzees and humans than to smaller bodied apes (e.g. gibbons). In fact, the Miocene can be regarded as the golden age of hominoids, with more types of these large primates living then than there are today.

The earliest apes are known as **dental apes**, i.e. apes with the dental (teeth) features of apes, but monkey-like postcranial skeletons. The dental apes were small compared with modern apes, were not adapted to brachiating (swinging from branches) and walked on the soles of their feet rather than their knuckles. For example, ***Proconsul*** (20 to 18 mya) has ape-like teeth, but a monkey-like limb skeleton adapted for running. These fossils from the Miocene therefore represent a complex picture of primate evolution and it is not yet clear how these types relate to modern apes. Fossils from this period have been found in Africa, Europe and Asia.

At about 17 mya Africa joined with Asia, allowing hominoid primates to migrate from Africa to Asia and molecular evidence suggests that the African great ape lineage (including human ancestors) diverged from the Asian great ape lineage (i.e. ancestors of orangutans) at about 14 mya. ***Sivapithecus*** (12 to 9 mya), from Turkey and Pakistan, shows facial features fairly similar to the modern orangutan. At about 7 to 5 mya, a huge primate appeared in Asia (***Gigantopithecus***) weighing up to 330 kg. An important final point concerning the Miocene is that no definite hominin (i.e. bipedal primate of human lineage) has yet been discovered from any Miocene locality.

Environmental conditions at the end of the Miocene favoured the more generalist monkeys over the apes. As forest areas decreased in size, monkeys adapted to terrestrial grassland environments, whereas most apes remained bound to their forest homes. The one exception to this is the lineage leading to humans (hominins), who adopted bipedalism (upright walking) and a precarious life on the forest fringes and grasslands.

Processes of macroevolution

As new environments become available, living things diverge to take advantage of new opportunities (e.g. the expansion of mammals at the beginning of the Cenozoic, or the diversification of lemurs in Madagascar). This process of **adaptive radiation** – the relatively rapid expansion and diversification of life forms into new ecological niches – depends on two factors: the adaptive potential of the species and the adaptive opportunities of the available zone. Absence of significant competition from other animals is an important factor in permitting wide diversification of living things as they enter new environments. Whether an animal has **generalized** features i.e. traits adapted for many functions, or **specialized** features i.e. traits adapted for only a narrow set of ecological functions, is important in determining the ability to respond to new environments. Usually only generalized organisms have the flexibility to allow rapid diversification. Highly specialized species have difficulty adapting to changing environments.

The single most important evolutionary factor underlying macroevolutionary change is **speciation** – the process by which new species are produced from earlier ones. Species are defined as reproductively isolated organisms, in other words only members of the same species can reproduce to produce fertile offspring. Isolation may be due to geographic factors (e.g. mountain ranges) or behavioural factors (e.g. differences in mating behaviour), with the first type of isolation usually preceding the second.

The traditional view of evolution emphasized the idea that change accumulates gradually (**phyletic gradualism**). Gould and Eldredge (1977) proposed that evolutionary change does not necessarily occur gradually. In this view (**punctuated equilibrium**) species may remain unchanged for thousands of generations and speciation occurs in spurts of only a few generations. To date primate evolution appears to proceed gradually in those groups where detailed study is possible, but this is not to say that punctuated equilibrium does not play a part in other unstudied primate lineages or in hominin evolution where small groups are isolated and environmentally challenged (see evolutionary pulse theory below).

The meaning of genus and species

If we define members of a species as organisms that can interbreed and are reproductively isolated from other organisms, then we will encounter problems when we try to define species in fossil material. Clearly, it is not possible to comment on the reproductive behaviour of bones. There will therefore be uncertainties about the boundaries of a given species both in time and space, uncertainties which can never be eradicated, no matter how complete the fossil record. This means that defining **paleospecies** must of necessity be arbitrary. Grouping into genera presents other problems, because usually a genus is defined as a group of species more closely related to each other than they are to species from any other genus. In living organisms one would perform breeding experiments to see if mules (sterile offspring) could be produced by breeding of species from the same genus (e.g. horses and donkeys). Clearly this is also impossible with fossil material. For fossil material we may use another definition for genus – species that are members of the same genus share the same broad adaptive zone. This may be assessed by reference to teeth structure because these body parts are often well preserved in fossils and indicate diet and ecology.

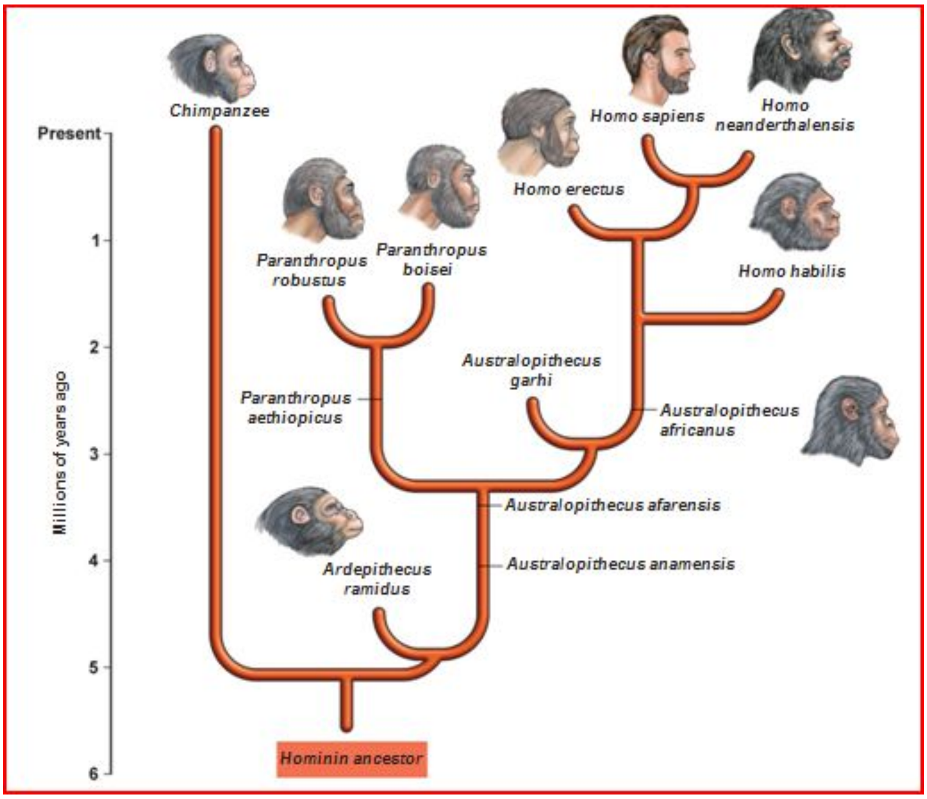
Lecture 7 Early hominins

Specific objectives:

1. To be able to define the term hominin.
2. To be able to summarize the main anatomical features of robust and gracile australopithecines and early genus *Homo*.
3. To discuss current thinking concerning the reasons for emergence of hominins from forest to savanna.
4. To summarize modern ideas concerning early hominin lineage and indicate reasons for uncertainty in these interpretations.

What is a hominin?

The terms **hominid** and **hominin** have been used for modern humans and their bipedal ancestors. Although hominid is a common term for human ancestors, it is not an optimal name because (based on genetic similarity) the family **Hominidae** includes humans, fossil humans, chimpanzees and gorillas. The tribe **Hominini** includes just modern humans and their fossil ancestors and so **hominin** is the preferable term for our immediate ancestors.



The most important defining characteristic of hominin evolution is the ability to perform bipedal locomotion comfortably. Other features such as neurological organization and behaviour (e.g. tool use, burial customs) become important in later stages of hominin evolution.

The first hominins or just apes?

Molecular evidence suggests that the first signs of homininization should appear in the late Miocene, but the fossil record with respect to this is particularly poor between 10 and 7 mya. Between 7 and 4.4 mya there are several candidates for the earliest hominin remains, but all or some of them may be apes rather than hominins.

In 2001, a French group discovered *Sahelanthropus tchadensis* (7.0 to 6.0 mya) in northern Chad. This specimen was nicknamed "Toumai" ("hope of life") and has hominin features (large browridge, smaller canine teeth, and a horizontally placed foramen magnum, which may indicate bipedality). The specimen also has apelike features (e.g. small brain size – 320 to 380 cm^3; a U-shaped dental arcade and thin tooth enamel).

In 1994, *Ardipithecus ramidus* (4.4 mya) was found in the northern Rift Valley of East Africa (Ethiopia). This region had dense forest inhabited by forest antelopes and the ancestors of modern colobine monkeys. The discoverers noted that the arm bones of this specimen bear similarities to both quadrupeds and bipeds and they were unable to say definitively how this primate walked. Subsequently (in 2004) the same group discovered *Ardipithecus kadabba* (5.8 to 5.2 mya) with more apelike features than *Ardipithecus ramidus*.

Later hominins from East Africa, from 4.2 mya to 1.4 mya, belong to another genus – *Australopithecus* (meaning "southern ape"). *Australopithecus anamensis* lived about 4.2 to 3.9 mya near lake Turkana in east Africa. This specimen is significant because it shows the first incontrovertible evidence for bipedality (large tibial plateau for carrying body weight). Another early example of this genus is the fossil known popularly as "Lucy" (*Australopithecus afarensis*) from Hadar in Ethiopia. *A. anamensis* and *afarensis* are more primitive than any of the other **australopithecine** fossils from Eastern and Southern Africa. Primitive features include longer upper limbs, large pointed canines, a lower first premolar that is semi-sectorial (i.e. it provides a shearing surface for the upper canine), and parallel rows of teeth (even converging to the back of the mouth in the case of *afarensis*). Average brain size for *A. afarensis* was probably only 420 cm^3. Note that some scientists consider that these two specimens belong in the same species.

Main anatomical features of robust and gracile australopithecines

Around 3 to 2 mya different varieties of australopithecine were present in Africa. These consist of several species that are usually divided into two main groups: robust and gracile australopithecines.

Robust australopithecines (*A. boisei*, *A. aethiopicus*, *A. robustus*) have large broad faces, very large molars and premolars, small incisors and canines, postorbital constriction between the facial bones and the brain case, flaring of the zygomatic arch and a sagittal crest down the midline of the skull. The sagittal crest and postorbital constriction probably are the consequence of large masticatory (chewing) muscles (**temporalis**) with a large area of attachment to the side and top of the skull. These anatomical features appear to be an adaptation to hard object feeding, i.e. chewing tough food items such as hard-shelled nuts and fibrous vegetation. The remains of robust australopithecines have been found in association with stone tools and the thumbs of robust australopithecines are like tool-making hominins, so they may have been intelligent creatures capable of making tools. Brain volume for robust australopithecines was about 510 to 530 cm^3. Note that some scientists include robust australopithecines in a genus of their own (*Paranthropus*).

Gracile australopithecines (e.g. *A. africanus, A. sediba*) had lightly built faces with rounded skull vaults, and with proportionately larger front teeth compared to back teeth than is seen in the robust australopithecines. Brain volume was about 410 to 480 cm^3. *A. africanus* was a small bodied biped that lived in woodland and open woodland environments. Another gracile australopithecine dated to 2.5 mya, *Australopithecus garhi*, has been found associated with butchered remains of animals, suggesting that they may also have used tools to scavenge meat. The recently discovered, almost complete, skeleton of *Australopithecus sediba* of South Africa has been dated at 1.9 mya.

Reasons for emergence of hominins from forest to savanna. Climatic factors in hominin evolution?

One model (the "**climatic forcing model**") postulates that as climates grew cooler in East Africa about 12 to 5 mya, forest cover became less continuous. This would mean that forest fringe habitats and transitional zones between forests and grasslands became more widespread. The model proposes that some late Miocene hominoids exploited the drier grassland portion of the fringe (the earliest hominins), while others concentrated more on the wetter regions (the ancestors of African great apes). In the protohominins, further adaptations would have occurred, such as bipedalism, increased tool use, dietary specializations (perhaps on hard items such as seeds and nuts) and changes in social organization. At present there is insufficient evidence to adequately test this idea properly, so the model, although plausible, can only be given tentative acceptance.

A related hypothesis concerning evolution among hominins is the **evolutionary pulse theory**. This idea arises from observations of spikes in the extinction of old species and the appearance of new ones (**speciation**). The model (a variant of punctuated equilibrium) suggests that there were periods during which speciation, not just of hominins, but also of other species (e.g. antelope), was particularly rapid in Africa. These occurred at 2.5, 1.8 and 1.0 mya and coincide with changes in the climate, in particular drying. The period around 2.5 mya is particularly interesting because this was a time of rapid change in hominins, including the first appearance of *Homo*.

Early *Homo* lineage

The earliest member of genus *Homo* also dates from the time of appearance of the robust australopithecines (2.5 mya). The defining characteristics that separate *Homo* from the australopithecines include: an increase in brain volume; less projecting face; smaller teeth; and eventually, larger body size and more efficient bipedalism. Louis and Mary Leakey identified the remains of *Homo habilis* ("handy man") at Olduvai Gorge as early as the 1960s. *H. habilis* had a cranial capacity (about 510 to 775 cm^3) extending outside the range of australopithecines (about 20% larger). Note that this indicates that there were at least two separate hominin lineages with many species existing side-by-side in Africa 2 mya. Some scientists consider that there was more than one species of early *Homo* (*H. habilis*, *H. rudolfensis* and *H. sp. nov*). The variability of early *Homo* may be due to climatic fluctuations at the time.

There are many interpretations of the evolutionary relationship of the various types of hominin present in eastern and southern Africa around 2 mya. It does appear likely that there were two main lineages, one leading to robust australopithecines, which eventually became extinct; the other leading to early humankind. Undoubtedly there were many smaller side branches of which we are not yet aware. The key difference between many of the proposed **phylogenies** (schematic representations showing ancestor-descendant relationships, usually in a chronological framework) is whether *A. afarensis* and/or *A. africanus* lie within the direct lineage leading to modern humans.

Lecture 8 *Homo ergaster* and *Homo erectus*

Specific objectives:

1. To summarize the major anatomical changes in the transition from earliest members of genus *Homo* to *Homo ergaster* and *Homo erectus*.
2. To indicate the type of climate during which *Homo erectus* emerged from Africa and diversified.
3. To be able to discuss the diversity of *Homo erectus* types throughout the Old World and indicate the significance of the wide dispersal of this hominin.
4. To be able to describe the key features of *Homo floresiensis* and its possible position in human phylogeny.

The origins of *Homo erectus*

Homo erectus was a widely distributed species that lasted over 1.4 million years. *Homo erectus* probably arose about 1.8 mya and the first dispersal of hominins in the form of *H. erectus* from Africa is now thought to have occurred between 1.7 and 1.8 mya. A fossil mandible from the Dmanisi site in Georgia has been provisionally dated at 1.8 to 1.6 mya and suggests that dispersal from Africa occurred as early as the origin of this species in East Africa. Some paleoanthropologists call the earliest *Homo erectus* from Africa and Southern Europe by the name *Homo ergaster*. *Homo erectus* eventually spread north to Europe and east as far as Java and northern China.

Homo erectus differed in several aspects from both earlier *Homo* and later *Homo sapiens*. Early *Homo* had cranial capacities ranging from 500 to 800 cm^3, but *H. erectus* had a cranial capacity of 750 to 1,250 cm^3 (with a mean of 900 cm^3). *H. erectus* also had a much larger body than earlier members of genus *Homo* - most males were about 1.7 to 1.8 m tall as adults. *H. erectus* was also quite robust (heavily built) in body shape and there was considerable sexual dimorphism, i.e. males were much bigger in body size than females. The trend in robusticity in the human lineage was to continue until the emergence of the relatively gracile modern *H. sapiens*.

Homo erectus had a heavily built skull, especially in those members living in northern Asia, large brow ridges (**supraorbital torus**), a thickened **angular torus** at the rear of the parietal bone; and a projecting **occipital torus** at the rear of the skull. The vault of the skull is long and low, receding back from the brow ridges with little forehead development. Most of the breadth of the skull is below the ear opening and the midline shows a sagittal keel, giving the skull a pentagonal contour when viewed from behind. The skulls of both earlier and later members of genus *Homo* had more vertical sides, with the maximum width above the ear openings. *Homo erectus* throughout the world also had incisors that were scooped out behind, giving them a so-called “shovel-shaped” appearance. This shape is thought to prevent damage when the incisors are exposed to heavy wear. The pulp cavities of the molars were particularly large.

Climatic conditions during the emergence and spread of *Homo erectus*

Homo erectus emerged during the early Pleistocene and disappeared before its end. The entire Pleistocene lasted from 1.8 mya to 10,000 ya and is also known as the Age of Glaciers or Ice Age. Large areas of the northern hemisphere were covered with enormous masses of ice, which advanced and retreated in a series of cycles. Early classifications of glacial Europe divided the Pleistocene into 4 major glacial periods. However, analysis of climatic changes throughout the Old World and North America indicate that there were actually about 15 major cold periods, or one major cold period every 100,000 years. Note that the last episode of glaciation was only about 10,000 years ago (the average duration of an interglacial), so it is entirely possible that the Pleistocene Ice Age has not ended yet!!

Homo erectus may have benefited from the harsh conditions of the Pleistocene. The locking up of water into the ice-sheets lowered sea level in the Indonesian archipelago, allowing dispersal of *H. erectus* into South-east Asia at least as far as east Java, and perhaps across to the island of Flores (see *Homo floresiensis*).

Diversity of *Homo erectus* types throughout the old world

Homo erectus fossil material has been found in China (Zhoukoudian, Yunxian, Lantian), Java, East Africa (Olduvai, East Turkana, West Turkana, Ethiopia), South Africa, North Africa and Europe (Dmanisi).

H. erectus from China possess typical features of the species as described above. Note however that there is some regional variation as well as variation in time. Cold climate and Javan *H. erectus* tend to have quite thick cranial vaults, while African forms have thin skulls. African forms are not as strongly buttressed in the cranium as the Chinese or Javan types. Supraorbital and nuchal tori are more pronounced in the eastern forms and these differences have prompted some to classify the African forms as a separate species – *Homo ergaster*. African forms like the boy from Nariokotome had long thin appendages, consistent with living in a warm climate, whereas the northern China types are more robust and shorter limbed.

There may also have been some cultural differences between Far Eastern *H. erectus* and other forms. The more advanced Acheulean technology is known from Africa as early as 1.4 mya and Western Europe and southwestern Asia for over 1 million years, but this culture has never been found in Eastern Europe or East Asia. In fact a distinct boundary, the **Movius line**, demarcates parts of the Old World where Acheulean hand axes were made from those where they were not. It is possible that other kinds of raw materials were used in China (e.g. bamboo) or perhaps the inhabitants of the Far East and Eastern Europe left Africa before the development of Acheulean technology.

Culture of *Homo erectus*

The most complete assemblage of cultural remains for *H. erectus* comes from China. The earliest stage (0.46 to 0.42 mya) consists of large tools, usually made of a soft stone like sandstone. The middle stage (370,000 to 350,000 ya) had smaller tools making up most of the sample. The final stage (300,000 to 230,000 ya) has small, high quality tools. No sandstone tools are present, only quartz of highest quality is used and flint accounts for 30% of the sample. Fragments of antler and bone, which had been hacked into pieces, were also found at Zhoukoudian.

There is still considerable debate as to whether *Homo erectus* was a true hunter or just a scavenger. Certainly evidence of butchering is present at many *Homo erectus* sites as early as 0.8 mya. *Homo erectus* was clearly a meat eater and the emergence of *Homo erectus* as a predator (as opposed to simply a scavenger) has been proposed as the enabling factor in the increase in brain and body size seen in the human lineage at around 1.8 mya. An intriguing alternative line of genetic evidence concerning this is that human tapeworms appeared to have diverged from hyena tapeworms at about 1.8 mya, presumably when ancient humans and hyenas shared infected carcasses. On the other hand, clear evidence is available that Peking man collected wild plant foods and this may have formed a large part of their diet. It has been suggested that eating of fire-cooked tubers may have provided an alternative source of high quality nutrients for enlarged brains.

Thick layers of ash have been found at Zhoukoudian (over 6 m deep in some parts) suggesting that the inhabitants used fire and hearths, but it is not known whether they could make fire or simply preserved a flame. Some authors contend that these ash layers are not evidence of habitation at all. Asian *Homo erectus* probably killed deer and horses and gathered berries, fruits and ostrich eggs. Awls for piercing hide and (probable) bone needles have been found, suggesting that some primitive clothing, perhaps poncho style, may have been made. Note that the climate of Beijing during the middle Pleistocene would have been particularly harsh during winter, so some form of clothing is very likely. Life expectancy was not high – 40% of bones are from individuals younger than 14 years and only 2.6% lived to 50 or 60.

Finally, there is intriguing evidence that *Homo erectus* may have been able to cross substantial bodies of water. Stone tools dated at 750,000 ya have been found on the island of Flores, 500 km east of Java and across what would have been open ocean at the time. If *Homo erectus* made these tools then some form of ocean-going craft (e.g. bamboo rafts) would have been required to reach this island.

The little people of Flores: a late population of *Homo erectus*?

Remains of a small hominin have been found in the Liang Bua cave on the Indonesian island of Flores. These remains were of several individuals dating as recent as 18,000 years ago, with one having a tiny cranial capacity of 380 to 420 cm^3. The specimen was given the scientific name of *Homo floresiensis*, but there are many features of the skeleton that are reminiscent of *Homo erectus*. The Flores hominins may be the result of **insular (island) dwarfism**, whereby large mammals that colonize small islands undergo a progressive shrinking of body size as a result of limited food resources and the absence of predators. Other scientists have argued that the small brain size of the Flores people is the result of a pathological condition known as microcephaly, and the small stature may be due to congenital deficiency in insulin-like growth factor. The precise significance of the Flores hominins remains to be seen and continues to engender controversy.

Films: Portrayals of human ancestors

Read the questions posed below before you watch these films. You will have the opportunity to discuss your impressions, especially during Practical 2.

Ideas about how human ancestors looked and behaved are often influenced by events and ideas in our own society. What is more, those ideas about human ancestors can often influence popular culture. In other words there is an ongoing interaction between the modern world and perceptions about human evolution. These two films illustrate examples of this interaction.

When watching the films (the opening scenes of *2001: A Space Odyssey* and the portrayal of australopithecines in *Walking with Beasts*) ask yourself the following questions:

- What ideas about early hominin behaviour are being portrayed in the film? What is being said about co-operation, aggression, social structure, tool use and upright walking?
- What has influenced the way that the hominins' behaviour is presented? Is it popular culture, the whim of the director/animator, reasoning by analogy from apes, or fossil evidence?
- Is there an attempt to convey a message of significance for the modern world? Is that message valid?

Lecture 9 Archaic *Homo sapiens*

Specific Objectives:
1. To be able to indicate the key anatomical features of early and late archaic *Homo sapiens*.
2. To be able to describe the cultural features of archaic *Homo sapiens*, with particular emphasis on European and Middle Eastern Neandertals.

Main anatomical features of early archaic types of *Homo sapiens*

Previously we discussed the anatomical features of *Homo erectus*. Many fossil finds from later Pleistocene Africa, China and Java display features that resemble both *Homo erectus* and *Homo sapiens*. These hominins are said to be archaic *Homo sapiens* (e.g. *Homo heidelbergensis*, or, less commonly, advanced *Homo erectus*!) and lived in the latter half of the middle Pleistocene from about 600,000 to 130,000 ya. During this period there is a transition from archaic to modern cranial features.

Early archaic *H. sapiens* exhibit changes from *H. erectus* - e.g. expansion of the brain beyond 1,200 cm^3, greater width of the skull above the ear (globular rather than pentagonal posterior profile), decrease in size of the molars and general decrease in the cranial and postcranial robusticity. A good example of this type is the Broken Hill (Kabwe) fossil, which has a large supraorbital torus, low cranial vault, and prominent occipital torus like *H. erectus*. Yet the cranial bones are thinner, the cranial capacity larger (1,280 cm^3) and the cranial base is more modern in form than *H. erectus*. Other examples of early archaic *Homo sapiens (H. heidelbergensis)* include the Bodo, Ndutu and Salé crania.

Late archaic *Homo sapiens*

Examples of late archaic *Homo sapiens* include the Neandertals of Europe and the middle East. These people take their name from the Neander river valley (valley = tal) in Germany, where the initial fossils were found. While some Neandertal remains have been found from as early as 130,000 ya, most data pertain to those living between 75,000 and 29,000 ya. One striking feature of Neandertals is the large size of their brains – while the average endocranial volume (ECV) for modern humans is 1,430 cm^3, for Neandertals it was 1,520 cm^3. The larger brain size may be associated with the greater metabolic efficiency of a larger brain in a cold climate. The Inuit (eskimo) brain also averages larger than that of other modern humans and is about the size of the Neandertal brain. In both ancient and modern populations, larger brain size is also correlated with larger body size in a cold climate. The Neandertal face stands out, their bodies were very robust, barrel-chested and powerfully muscled. Supraorbital ridges are prominent with a low forehead and the back of the skull has an **occipital bun**. There is pronounced midfacial prognathism. Related to this is the forward displacement of the teeth, resulting in a **retromolar gap** between the third molar and the ascending ramus of the mandible. The mastoid process of Neandertals is smaller than in modern humans, but a ridge of bone near the mastoid process, the **juxtamastoid eminence**, is larger than the mastoid process. The chin is absent and there is no canine fossa over the upper canines. The piriform aperture (nasal opening of skull) is high and wide. Neandertal molars tend to have extra cusps compared to modern humans and expanded pulp cavities (**taurodontism** – literally “bull-teeth”); incisors are shovel-shaped (as seen for *Homo erectus*) which may be an adaptation to reduce the impact of heavy wear on the pulp cavity. Limbs appear shorter than in modern humans, also consistent with life in a cold climate (Allen’s rule). It is likely that

European Neandertals lived alongside anatomically modern humans for some time (from about 35,000 ya to 29,000 ya).

Neandertal genetics

How closely related to modern humans were the Neandertals? Did Neandertals contribute genetically to modern European populations? The cold climate occupied by Neandertals and the preservation conditions of their remains have allowed the survival of their genetic material in fossils. Mitochondrial DNA of Neandertals is different from modern humans, but the nuclear DNA of Neandertals did make some contribution to modern human populations, mainly with respect to genes concerned with skin pigmentation and keratin production. On the basis of genetic (dis)similarities, divergence of Neandertals and modern humans is thought to have occurred between 365,000 and 853,000 years ago, but with some re-mixing when modern humans emerged from Africa. Ancient DNA also suggests that some Neandertals had pale skin and red hair, which would be adaptations to a low-sunlight environment and difficulties acquiring vitamin D.

Culture of archaic *Homo sapiens*

Early archaic *H. sapiens* is associated with the same Acheulean culture used by *H. erectus*. Archaic *H. sapiens* lived in caves and open air sites and certainly controlled fire. Many different types of food were used (fruits, vegetables, seeds, nuts, bird eggs, fish and small to large mammals). Wooden spears made of spruce and finely balanced have also been found in association with remains of early archaic *H. sapiens* and have been dated to 380,000 ya. These strongly suggest that advanced hunting skills were possessed by these early *H. sapiens*.

Early Neandertals are often associated with **Mousterian** culture (see lecture on the hand), whereas later Neandertals are associated with an upper paleolithic technology, the **Chatelperronian**. There do not appear to be many bone tools associated with them, unlike the technology of modern humans in the Upper Paleolithic. People of the Mousterian culture lived in open sites, caves and rock shelters. When they lived in the open they built huts or tents out of skins and mammoth bones. When they lived in caves they built windbreaks of poles and skin erected at the cave mouth. Neandertals used close-proximity spears to hunt and so were very prone to injury when hunting large mammals. Berger and Trinkhaus (1995) showed that the injury pattern of Neandertals (high incidence of head and neck injuries) closely matched those of modern rodeo performers! The “Old Man of La Chapelle-aux-Saints” was found buried in a cave in the Dordogne region of southern France. This individual had had a hard life and was probably about 40 years of age (!). He suffered from several pathological conditions (missing teeth, thinned mandible from tooth loss, deformed pelvis, crushed toe, arthritis in vertebrae, and a broken rib). Survival with these problems indicates a supportive social structure and perhaps some assistance with pre-mastication of food.

Anatomically modern humans replaced European Neandertals. It is useful to compare the cultures of the two to try to understand why this happened.

	Neandertals	**Upper Paleolithic *H. sapiens***
Tool technology	• Few tools which have highly specialized functions. • Use of bone, antler, or	• Many highly specialized tools. • Frequent use of bone, antler and ivory.

	ivory very rare. • Few tools with more than one or two parts.	• Many tools comprised of two or more parts.
Hunting efficiency and weapons	No long distance weapons – all close proximity weapons (stabbing spear)	• Use of spear thrower, bow and arrow • Wider range of social contacts possibly with larger, more organized hunting parties.
Stone material transport	Stone materials transported only short distances.	Evidence for widespread stone transport, suggesting perhaps trade and wide social contacts.
Art	Art uncommon. Usually small.	Artwork much more common, including elaborate cave art and transportable objects (e.g. Venus of Willendorf). Stylistic sophistication using a variety of materials and techniques.
Burial	Graves unelaborated and frequently lack artifacts (grave goods)	Burials much more complex, frequently with grave goods (tools, clothing) also remains of animals.

The mysterious Denisovans

These are an extinct species of human in the genus *Homo*. The name is based on a bone that was found in the remote Denisova Cave in the Altai Mountains in Siberia. The discovery in March 2010 was of a finger bone fragment of a juvenile female who lived about 41,000 years ago. Two teeth and a toe bone belonging to different members of the same population have since been reported.

Analysis of the mitochondrial DNA (mtDNA) of the finger bone showed it to be genetically distinct from the mtDNAs of Neanderthals and modern humans. Denisovans are believed to share a common origin with Neanderthals. They ranged from Siberia to Southeast Asia, and lived among and interbred with the ancestors of some present-day modern humans, with about 3% to 5% of the DNA of Melanesians and Aboriginal Australians deriving from Denisovans.

Lecture 10 Modern *Homo sapiens*

Specific Objectives:

1. To be able to discuss the two main models concerning the emergence of anatomically modern humans, describing the evidence for each.
2. To be able to indicate the main upper paleolithic archaeological sites for *Homo sapiens sapiens*.
3. To be able to list the anatomical features of modern humans that distinguish them from archaic *Homo sapien*s.

The emergence of anatomically modern *Homo sapiens* from archaic forms (complete replacement vs regional continuity models)

There are two models advanced to explain the emergence of anatomically modern humans from archaic H. sapiens.

The first is the **complete replacement model**. It was developed by British paleoanthropologists Christopher Stringer and Peter Andrews in 1988 and is based on the origin of modern humans in Africa about 200,000 ya and the later ***complete*** replacement of populations in Europe and Asia ("Out of Africa" model). It considers the appearance of anatomically modern humans as a biological speciation event. In other words there was no mixing between migrating African modern *H. sapiens* and local populations because the African modern humans were a biologically different species. Support for this model has come from genetic data obtained from living peoples. Using mitochondrial DNA (Wilson, Cann and Stoneking - 1987), which is inherited from the mother by each generation ("Mitochondrial Eve"), and variation in the Y chromosome (Dorit et al., 1995), which is inherited from the father, several groups of scientists have claimed genetic data support for the complete replacement model. The mitochondrial DNA studies found that African mitochondrial DNA contained only African variants, whereas mitochondrial DNA from other areas of the world contained at least one African component. This was interpreted to mean that all modern humans outside Africa arose from a single population within Africa. Note that this interpretation remains controversial and many other studies have reached different conclusions. Nevertheless it does appear that modern humans outside Africa are genetically homogeneous, consistent with a recent origin from a (predominantly) single source.

The **regional continuity model** (multiregional evolution) was developed by Milford Wolpoff and others (Thorne and Wolpoff, 1992; Wolpoff et al., 1994). These researchers suggest that local populations in Europe, Asia and Africa continued their indigenous evolutionary development from archaic *H. sapiens* to anatomically modern humans. For this to have occurred there must have been considerable gene flow between populations of ancient humans. This means that anatomically modern humans could not be considered to be a separate species from archaic forms.

An intermediate form of model is the partial replacement model where anatomically modern humans emerged from Africa and interbred with archaic forms to produce hybrids. Most recently, molecular studies suggest that there has been some admixture of archaic and modern Homo sapiens DNA (only a few % of archaic), so the intermediate form with a major contribution of African DNA is the most favoured model currently. Eventually the modern human polytypic form appeared, but only after a complex process of migration and interbreeding between modern and archaic populations.

Major archeological sites for anatomically modern humans

- *Africa – These sites include the Klasies River Mouth, Border Cave in South Africa; and Omo Kibish 1 in southern Ethiopia.*
- *Near East – Skhul cave at Mt Carmel, Qafzeh cave.*
- *Central Europe – Vindija in Croatia, Mladec in the Czech Republic.*
- *Western Europe – Cro-Magnon in the Dordogne of southern France.*
- *Asia – Zhoukoudian near Beijing and Ordos in Inner Mongolia.*
- *Australia – Kow Swamp and Willandra Lakes.*
- *Americas – Several sites have been identified, but controversy persists about dates.*

In many of the Old World sites, Neandertals are found inhabiting the region or even the same cave in earlier times. In some sites (Vindija, Qafzeh) the fossil remains show signs of a mixture of Neandertal and modern features supporting the regional continuity hypothesis. Significantly, the Jinniushan skeleton from north-east China has been dated at 200,000 ya and has been claimed to have modern features. If this is true then the complete replacement model could not be correct.

Anatomical features of modern humans

Anatomically modern humans showed **vertical foreheads**, relatively **small browridges**, **canine fossae** below the orbits, a **pyramidal mastoid process**, **small anterior teeth** and a **definite chin**. The canine fossa, prominent chin and small teeth are all linked in that the two former are consequences of the latter, i.e. recession of the dental arcades as teeth became smaller led to smaller maxillary and mandibular alveolar margins.

Upper paleolithic culture

Upper paleolithic culture began in western Europe about 40,000 ya and is usually divided into five different industries based on stone tool technologies (Magdalenian, Solutrean, Gravettian, Aurignacian and Chatelperronean from youngest to oldest). The upper paleolithic was a period of rapid technological advance and cultural richness unlike anything seen before. In Europe and central Africa in particular, there were profound cultural changes that saw big game hunting, potent new weapons (spear-throwers, harpoons and possibly bow and arrow), cave "art", body ornaments, needles, "tailored" clothing and burials with elaborate grave goods.

Climatic conditions of the upper paleolithic in Western Europe

A warming trend in much of Eurasia saw the appearance of a vast area of treeless country dotted with lakes and marshes. During the short summers there was abundant growth of flowering plants and mosses, providing pasture for large herds of grazing animals. People exploited fish and birds systematically for the first time and upper paleolithic people spread across Europe living in caves and open-air camps as well as building shelters.

Cultural adaptation to harsh environments

Tailored clothing allowed modern humans to occupy for the first time the harsh environments of far northern Europe and northeast Asia. This was probably possible because of better constructed shelters as well as tailored clothing. The evidence for the latter comes in the form of pointed stone tools such as awls, which allow the puncturing of hides, and bone needles for sewing.

Upper paleolithic tools. What do they tell us about the people who used them?

There are many different tool technologies from the upper paleolithic (40,000 to 10,000 ya) because this was a period of rapid advance. Tools from the upper paleolithic are different from earlier cultures in several ways:

- They show much more sophisticated workmanship. Pressure flaking techniques were developed and used to make beautiful parallel-sided lance heads. The punch-blade technique allowed the manufacture of an abundance of standardized blank stone flakes that could be fashioned into burins for working wood, bone and antler; borers for drilling holes in skins, bones and shells and blades for knives with serrated or notched edges for scraping wooden shafts into a variety of tools.
- They often use combinations of materials (e.g. bone, sinew and wood, or wood and ivory).
- They may also have served as works of art or cultural symbolism. Some stone tools dating from this period were so delicate that they would have broken in ordinary use. Even utilitarian tools were decorated by carvings.
- They represent significant technological advances e.g. the atlatl or woomera (for extending the period of acceleration of a thrown spear), harpoons (spears with detachable heads to hunt aquatic prey), perhaps the bow and arrow, sewn clothing.
- The first experimentation with fired pottery has been reported to date from this period (small animal figures from two sites in the Czech Republic dated at 27,000 ya).
- Several authors have claimed that textiles were first used at this time, based on the appearance of carved figurines such as the Venus of Willendorf.

The **Magdalenian** (17,000 to 10,000 ya) was a period of remarkable technological innovation. The spear-thrower (atlatl, woomera) appeared for the first time. By effectively increasing the length of the thrower's arm it allowed increased force, distance and accuracy to spear throwing. Fish were caught with barbed harpoons and the bow and arrow may have appeared for the first time. While most of the year would have been spent in small groups of 25 people or less, there would have been times when upper paleolithic people came together for special festivals forming aggregations of up to 500 people. It is also notable that some simple industries began at this time – notably the bead-making industry of southern France - and that there was substantial trade for rare and significant raw materials (obsidian) and finished items (bead work).

"Art work" of the upper paleolithic

People of the upper paleolithic are also noted for their "art work". This would take the form not only of cave paintings, but also of small carved figurines. Another significant area of which we have only a little evidence is music – simple bone flutes have been found indicating the origins of musical expression at this time.

It is important to be careful in our interpretation of visual imagery like cave painting and figurines. It is natural for archeologists from modern culture to impose their own interpretation on cave paintings, assuming that the goal was to create aesthetically pleasing images. But it should also be remembered that even in our own culture visual images can be intended for purely utilitarian purposes (e.g. traffic signs, advertising) and we really do not know precisely what the purposes of the early cave artists were.

Cave painting which dates to the upper paleolithic has been found throughout Europe, Siberia, North Africa, South Africa, Australia and the Americas and shows a wide variety of styles distributed both in space and time. Famous examples like the Lascaux and Grotte Chauvet caves of southern France and northern Spain have been preserved because the cave-painters chose to perform their work deep underground. It is certain that other peoples from around the world also prepared cave-paintings, but may have done so close to the surface, with the result that the work has long since been eroded.

A familiar cave painting motif from around the world is the stencilled hand, which has been seen in Europe, the Americas and Australia. This is produced by the artist blowing pigment onto and around a hand placed against the cave wall.

Small sculptures ("portable art") date back to at least the beginning of the Aurignacian (35,000 ya) and originally consisted of carved handles to implements. Examples have been found throughout Europe. Bone and ivory were the materials of choice and required special stone tools. Particularly famous examples include the Venus of Willendorf and the Venus of Brassempouy. The symbolic significance of these remains uncertain; perhaps they were fertility symbols, perhaps they were considered important in protecting women during childbirth.

What is the significance of the artwork of the upper paleolithic? It has been argued that the pictorial representations of animals and humans had some association with religious ritual and magic with the purpose of improving or celebrating hunting, but not all animals represented were subject to hunting. It is notable that many groups of animals were painted in caves with the best acoustics, suggesting some role in rituals involving spoken language or chanting. It is also interesting to note that most of the cave art was created during a period of severe cold, when the caves may have provided refuge and meeting places during certain times of the year.

Lecture 11 Humans in Australia

Specific Objectives:

1. To indicate scientific evidence concerning the antiquity of human occupation of Australasia.
2. To be able to describe possible routes and technological developments associated with human migration into Australasia.
3. To be able to summarize fossil evidence of prehistoric humans in Australia, discussing the similarities and differences between these humans and other human fossils of similar antiquity elsewhere in the world. How did these ancient human populations contribute to modern aboriginal populations?
4. To be able to summarize major geographic, climatic, floral and faunal conditions in Australia 60,000 years ago and indicate how these would have affected human occupants of our continent.
5. To discuss the impact of ancient human occupation on the Australian environment.

The antiquity of human occupation of Australia

Humans are thought to have colonised Australia between 40,000 and 70,000 years ago, although some evidence suggests it may have occurred before 100,000 years ago. The oldest sites are found at Lake Mungo in southwest New South Wales, and Malakunanja and Nauwalabila in the Northern Territory. Human remains from Lake Mungo, the "Mungo Man", have been directly dated using multiple techniques to older than 60,000 years. Recent re-dating of sediments at Lake Mungo has suggested the younger age of only about 40,000 years old. The debate about the true age is ongoing and best estimates remains at 40,000 to 60,000 years old. Given the location of Lake Mungo in the southeast corner of Australia it seems likely that humans arrived on the Australian continent before 50,000-70,000 years ago. The archaeological sites of Malakunanja and Nauwalabila were occupied between 50,000 and 60,000 years ago and provide confirmation of the older dates at Lake Mungo.

In 1996 the site of Jinmium in the Northern Territory was on the front page of newspapers all over the world. Australian scientists claimed that Australia had been occupied for about 170,000 years following dating studies at this site. Recent research has shown that the site may only be about 10,000 years old and that the materials dated in the original study had been contaminated by older, non-archaeological rocks.

Human migration into Australia

Humans must have entered Australia by sea-routes, since there has never been a direct land connection between Australia and Southeast Asia even during the periods of lowest sea-levels (see below). Nevertheless, during the last glaciation, the sea crossing would have been much easier than currently, with only a few hundred km of open ocean. It has been suggested by Alan Thorne (of the ANU) that the early Australians used bamboo rafts to cross from Southeast Asia. Bamboo provides a water-tight material with good buoyancy and is readily available to people of Southeast Asia. Once the initial sea crossing was completed, it appears that most campsites from this early time were along the coastline, where abundant marine and coastal life provided a rich source of food. The continental interior was even drier than at present and probably was relatively inhospitable.

Fossil evidence of prehistoric humans in Australia

There appear to have been two main types of humans present in early Australia. In the 1920s, during work on the Murray River Irrigation Project, several fossils were found at **Kow Swamp** in northern Victoria. Their significance was not realized until the early 1970s when Alan Thorne happened to inspect their bones at the Museum of Victoria. Following excavation at Kow swamp, the remains of about 40 individuals were found. These people probably entered Australia about 20,000 years ago. All the people were very robust, with thick skulls, large faces, large protruding teeth, and thick brow ridges which in some cases formed a complete buttress over the eye sockets. Their foreheads were flat and sloped back to a low posterior crown. These people had similar cranial features to those seen in Indonesia at earlier times and similar fossils have also been found in Cossack in Western Australia and Talgai in Queensland. These finds suggest that at least some of the early Australians came from Indonesia, but this is not the full picture.

In 1968 further human remains were found at **Lake Mungo**, one of the Willandra lakes in western New South Wales. One set is of a woman who was apparently cremated more than 40,000-60,000 years ago – the earliest cremation known anywhere in the world. The bones are remarkably delicate, so thin that the fragments were originally thought to be emu egg shell. The Lake Mungo woman had a skull that was remarkably modern, with a vertical forehead and teeth that do not project forward. In 1974 a site (of the same age as Lake Mungo 1) with the burial of a man was found nearby.

The gracile population at sites like Lake Mungo represent the earliest people to inhabit Australia before 50,000-70,000 years ago. It seems likely they represent a group of people who migrated to Australia via island southeast Asia (Philippines through to New Guinea). At the site of Liujiang in China, human remains that are morphologically identical to the gracile remains of Australia have recently been dated to well over 100,000 years old. This strongly suggests that the earliest Australians either originate from southern China or were descended from a population distributed widely across Asia more than 100,000 years ago. A second group of people inhabited Australia sometime after 30,000 years ago. These robust people, found at sites like Kow Swamp, show strong anatomical similarities to people who inhabited Indonesia, perhaps for several hundred thousand years. Modern Aboriginal Australians are descended from both of these populations as well as other people who arrived in northern Australia over the past few thousand years. Even Polynesian explorers are known to have landed in Australia, with archaeological remains found on the South Coast of New South Wales. Australia, like many other parts of the world, has a complicated and dynamic population history, despite its relative geographic isolation.

Geographic, climatic, floral and faunal features of Australia during the last 40,000 years

The Australia of 50,000-70,000 years ago was a very different place from the one we know today.

From about 45,000 years ago, the world was in the grip of a severe Ice Age period which lasted until 10,000 years ago. The Ice Age was at its most severe at about 18,000 years ago, at which time sea levels were 150 m lower than they are today. The present day sea level was reached only 6,000 years ago. Just before the height of the last glaciation, when the first people entered our continent, Australia, New Guinea and Tasmania were joined in a continent known as Greater Australia (or **Sahul**).

The climate was quite different in this ancient Australia compared to present times. The snow line was as much as 1,000 metres lower than at present and the interior of the continent would have been cooler and drier than currently. The Gulf of Carpentaria was occupied by a broad grassy plain dotted with hills. The centre of this plain contained a large freshwater lake (Lake Carpentaria) which was about 500 km by 250 km, fed by rivers but probably filled with brackish water. The area now occupied by the Great Barrier Reef was also a flat plain, extending almost to the edge of the continental shelf. Coastal plains extended down the eastern and western coast, with hills where the present offshore islands lie. Sydney Harbour was a deep valley cut into a sandstone escarpment by rivers. Tasmania was linked to the mainland by a pair of land bridges, which flanked the freshwater Lake Bass (250 km long). There was also a wide, very flat plain filling the Great Australian Bight. The two large freshwater lakes of it would have supported rich fish populations and huge colonies of birds. A similar rich source of food would have been provided by a chain of smaller freshwater lakes, extending from South Australia to Lake Carpentaria across the eastern third of the continent.

The central western part of Greater Australia would have been even more desiccated than presently. This was a time when fierce winds built up the sand dunes which today extend across large areas of the western inland. The rainforest, which had once covered the entire continent, had by this time retreated to the eastern coast and extended from northern Queensland to Tasmania. Drought-adapted and fire-resistant eucalypts were the dominant trees in other wooded areas. Across the northern part of the continent lay a region which had been colonized by many plants (Mangrove swamps, yams, and Pandanus groves) from the Indo-Malaysian islands.

Similarly, many animals of the northern parts of Greater Australia resembled those present in Southeast Asia, but further south the fauna was dominated by marsupial megafauna (e.g. herbivores like *Diprotodon* and *Procoptodon*, and carnivores like *Thylacoleo* and *Thylacinus*).

At about 15,000 years ago, the glaciation finished and sea levels began to rise, inundating the coastal plains and river valleys (e.g. Sydney harbour). The overall climate became slightly moister and warmer, although the western two-thirds of course remains extremely arid to this day. Dry sclerophyll forest and scrubby open woodland remain the dominant vegetation. The megafauna became extinct.

The impact of ancient human occupation on the Australian environment

The period of human occupation of Greater Australia saw the extinction of the megafauna. It is highly likely, though not definitively proven, that humans contributed to this in some way. Certainly the importation of the dingo about 4,000 to 5,000 years ago coincided with the decline of the marsupial predators *Thylacoleo* and *Thylacinus* on the mainland.

Australians modified the landscape to their benefit by practicing “firestick farming”. The periodic burning of grassland (once every few years) produced new green shoots, attracted game, and made the country easier to cross for hunting. Early European sketches and paintings showed the area of Sydney as an open, park-like landscape of scattered trees and short grass. This has been assumed to be the result of an attempt to Europeanize the portrayal of the landscape, but may have actually been the real landscape. Since Europeans prevented regular burning, vegetation patterns changed to tangled horizontal scrub. This in turn contributes to the catastrophic fires seen from time to time in Eastern and Southern Australia.

How many Australians were there when Europeans first came and what became of them?

There may have been as many as one million indigenous Australian peoples at the time of European invasion. Many of these peoples died in large numbers as a result of introduced European diseases like smallpox. In fact, it is estimated that half of the Sydney region native Australians died in 1789 as a result of that disease. By the time that Mitchell or Sturt made their journeys into the interior and reported on the population sizes there, as many as 75% of the native population may have already died. The actions of squatters contributed to further declines during the 19th century.

Lecture 12 Humans in the Americas

Specific Objectives:

1. To be able to indicate the probable Old World origin of Native American people.
2. To be able to discuss and contrast conflicting viewpoints on the mode and timing of entry of Native American people into North America.
3. To be able to summarize findings from key archeological sites pertaining to North American prehistory.
4. To be able to discuss domestication of animals and plants in the Americas.
5. To be able to discuss the linguistic and cultural diversification of Native American people, relating culture and technology to environment and resources.

Introduction: the old world origin of native American peoples

From about 80,000 ya until 10,000 ya (Wisconsin glaciation), the Pacific Ocean was at least 25 m shallower than it is today and for most of that time the sea level was 50 m lower than the present level. This would have resulted in exposure of the shallow floor of the Bering Strait between Asia and North America to produce a broad plain known as Beringia. Even when the sea level was only 25 m lower, the Bering Strait would have consisted of only a narrow waterway a few kilometres wide. For much of this period, Beringia would have been an extension of the Siberian tundra, with the same vegetation and herds of grazing animals. At its eastern end, Beringia would have met the mountains of Alaska, with sheltered valleys for grazing herds in winter. It is likely that both the migrating herds and the ancient Siberian peoples who followed them, would have moved backwards and forwards across Beringia throughout the year. It is highly likely then, that modern Native Americans are derived from the hunter-gatherers of northern Asia, although other alternative hypothetical origins have been proposed. Native Americans from both continents certainly have facial features which suggest an Asian origin, although most of them do not have the same extreme flattening of the nose as seen in modern north Asian people. The nasal flattening is an adaptation to cold (minimizing the chance of frostbite) which must have appeared after the migration of the first Native Americans across Beringia. All Native American groups have a high incidence of shovel-shaped incisors and three-rooted molars, both characteristics of modern Asian people. Some native American groups show a pronounced mongolian eye-fold, while others do not, but this is a feature, which probably had not fully developed by the time of migration into the Americas.

The time and mode of entry of Native American ancestors into North America

The approximate date when people crossed Beringia into North America is a contentious issue. One problem is that the route, which would have been followed by these people, is currently under water. Originally, most archeologists working in this field would have considered that the earliest reliable human remains from North America date to only 14,000 ya. It has traditionally been thought that during the cold phase there were two main ice sheets in North America – one centred on Hudson Bay, the other on the mountains of north-west Canada. The latter ice sheet would have provided an impassable barrier to human migration into North America until after the peak of the ice age, when the ice cap began to shrink and an ice-free corridor opened up through Canada. Other authors have argued that the ice sheets were perhaps not as extensive as previously thought or that ice sheets may have covered different areas at different times, thereby allowing humans to have moved from one ice free region to another to progressively reach the heartland of North America.

Rock shelter sites in north-eastern Brazil (Pedra Furada) have been dated to indicate human occupancy from 32,000 to 17,000 ya. Other sites in the Andes and Pennsylvania have been dated at 20,000 ya. On the basis of these findings some authors have proposed that humans entered North America as early as 40,000 ya, although this remains a controversial area. Native Americans in both continents can be divided on the basis of morphology and language into three groups, perhaps indicating three waves of migration. The largest group consists of all people in South America and most of the North Americans (south and eastern parts). These people are least like modern Asians and probably entered the Americas first. The second group consists of people in the north-west of North America, from just south of the Canadian border up to Alaska. These people are more like modern people of eastern Asia and Siberia than the first group. The third group includes the Eskimos of Greenland, Canada and Alaska and the Aleuts of the Alaskan peninsula and the Aleutian islands, and is most like Asians.

The first immigrants were originally thought to have been overland explorers, using the land bridge to enter North America and then waiting for an ice-free corridor to open to allow them to move further south into the heartland of the continent. An alternative idea is that the first immigrants used the coastal root to enter North America, avoiding the ice sheets and relying on abundant marine life during their movement east and south. If the latter is correct, then colonisation may have initially proceeded down the coast even into South America before the interiors of either continent were entered.

Specific remains

Kennewick man is the 9,000 year old remains of a male aged about 40 years, who lived in NW North America. Kennewick Man's skull morphology cannot be categorized into any major populations today, but most closely resembles Pacific Rim populations such as the Ainu of Japan and Polynesians, reflecting deep roots of indigenous Americans in coastal Asian groups.

Ice age overkill

Today there are 15 species of large mammals in North America, but at the time at which the last ice age ended there were over 70 (mammoths, mastodons, sabre-toothed cats, giant bears, bison, camels, horses, and six metre long, 3 ton ground sloths!). It has been estimated that there may have been 50 to 100 million large mammals north of Mexico. These animals disappeared during a relatively short interval about 11,000 ya and this mass extinction is generally attributed to a group of people called the **Clovis hunters**, so named because of the large, finely made stone hunting points found at Clovis in New Mexico. It is possible that climatic changes may also have played a part and it may be that these changes put certain species under such environmental stress through loss of habitat, that even a few hunters could have pushed them to extinction. Introduction of pathogens with humans may have also been a factor.

Later tool cultures (**Folsom** - 11,000 to 10,000 ya) appear to be adapted for hunting smaller game. Folsom spearheads have a longer flute on a shorter spear-point than Clovis and are associated with smaller mammals including small bison.

Key archeological sites in North American prehistory

- Meadowcroft, Pennsylvania – Evidence for the time at which humans crossed the Rockies into eastern North America comes from a cave site on the Ohio river near Pittsburgh, where stone tools and charcoal heaths have been found. The bones of deer, chipmunks and squirrels which were apparently hunted in the deciduous and conifer forests have also been found here in sediments dating through the period from 19,000 to 12,000 ya.

- “Head Smashed In” is a site 100 km south of Calgary and illustrates the hunting techniques of the plains people. The Piegan people here had worked out a means of killing large numbers of buffaloes in relative safety. The site has a high sandstone cliff facing the plains. Back from the clifftop is a shallow, well-watered basin where herds of buffalo often gathered to feed. The Piegan hunters would creep up behind the hills and form a huge arc slowly moving the buffalo down the valley towards and over the cliff. At the bottom of the cliff other people waited to butcher the dead and dying animals. This site was used for several thousand years – so long that the grassy slope at the foot of the cliff is a bed of buffalo bones more than 10 metres thick.
- Chaco Canyon is a wide shallow depression in the desert of New Mexico and was the site of an urban development by the Anasazi people at about 1,000 ya. The region was covered by a system of roads and small towns covering more than 50,000 km2. The most impressive is Pueblo Bonito, set against the north wall of Chaco Canyon, which includes a 5 storey building with 650 rooms. Later developments were built at Mesa Verde in Colorado. The Anasazi city system appears to have collapsed during the 13^{th} century AD, apparently due to climatic changes associated with the “Little Ice Age” which gripped the northern hemisphere for 300 years.
- Mound builders of the Mississippi and Ohio river valleys. When Europeans first entered these river valleys they encountered many mounds, some up to 30 m in height and others shaped like birds and mammals. These were apparently built from 2,500 years ago. Excavations of the burial mounds have revealed polished stone axes and mace heads, flint and obsidian arrow heads, carved stone tablets and smoking pipes, pottery statues, animal and human figures cut from sheets of mica, carved shells from the Gulf of Mexico and copper objects from the Great lakes (where people had begun to hammer native copper into useful and decorative shapes). These people built a city state at Cahokia, Illinois and had a trading network which extended from the Atlantic to the Great Plains. One of the most famous mound excavations is the Dickson mound in Illinois, where 250 skeletal remains dating back more than 1,000 years were found. Many of these skeletons show evidence of tuberculosis and osteoarthritis as well as malnutrition and anemia during childhood. The remains of the Dickson mound spans the period from hunter gatherer existence to the beginnings of agriculture (maize cultivation – see below) and indicate that this transition was accompanied by serious health consequences due to both nutritional problems and overcrowding.

Domestication of plants and animals

Corn appears to have been first domesticated in Mexico, about 7,000 ya. The knowledge and seeds necessary for its cultivation spread north into the south west of North America about 2,000 ya. Mesoamerican people also domesticated beans, chili peppers and avocados, as well as wild dogs and turkeys, some time between 10,000 and 7,000 ya.

In South America, domestication of lima beans, cotton and squash probably occurred in lowland Peru about 6,000 ya, while domestication of the potato probably began in upland Peru about 7,000 ya. It is interesting to note that all of the wild relatives of the potato have varying degrees of toxic alkaloids, so domestication of the potato probably involved a great deal of careful selection of non-toxic variants.

Andean people tamed the wild guanaco and produced two domesticated animals from it – the llama and the alpaca, while the guinea pig became a staple meat source which could live in the people's mud brick homes and be fed on scraps. In the Amazonian basin, pineapples, peanuts, passionfruit, arrowroot and cassava were all domesticated.

Diversity of Native American peoples

The people of the Americas show a remarkable cultural diversity which has been greatly influenced by the environments they inhabit.

Living under adverse conditions, the people of Tierra del Fuego are the most southerly of all humans. The southern tip of South America is extremely cold in winter, with powerful winds (the roaring forties) which strip forest trees. The swampy ground holds no edible roots or burrowing animals and the streams flowing out of the bogs have very few fish or crustaceans. The Ona people, who live around the Straits of Magellan, are nomadic people who hunt guanaco almost exclusively. They have never used canoes, harpoons or fish spears and have very little vegetable food in their diet.

The "Fuegans" can be contrasted with the people of Peru, who domesticated many animals and plants in both the high- and lowlands and built an advanced civilization. Clearly cultural development has been determined to a large extent by availability of resources and clemency of the climate.

Lecture 13 Evolution of human behaviour

Specific Objectives

1. To be aware of the promise and hazards of evolutionary interpretations of human behaviour.
2. To be able to discuss the biological and cultural bases of ideals of physical beauty and attractiveness.
3. To be able to discuss common mating systems in human societies.
4. To indicate the widespread use of psychoactive substances by humans and give an example of a genetic factor that may modify the risk of substance abuse.
5. To define depression and schizophrenia and to place them in an evolutionary context.

Interpreting modern human behaviour in an evolutionary context

Since much of human history was spent as scavengers and/or hunter gatherers, it seems logical to attempt to understand our modern behaviour in an evolutionary context (**Environment of Evolutionary Adaptiveness - EEA**), particularly where those behaviours appear to be widespread throughout all human societies and are not culturally specific.

Unfortunately, 19th and early 20th century evolutionary interpretations of human behaviour were often used to justify racist and sexist ideologies, so we need to apply rigorous logical criticism to such interpretations.

In any individual, behaviour is the result of a complex interaction between genes and environment. Although genetic factors may contribute to undesirable behaviour or illness, this does not void the responsibility of society and governments to optimize the environment in which such behaviours emerge.

The evolutionary basis of ideals of physical beauty and attractiveness

Among mammals, females are the gender which must make the greatest physical investment in reproduction, because they must gestate and breastfeed the offspring. From evolutionary theory, we would expect that each sex would adopt strategies that allow them to maximize the chances of their genes being transmitted to the next generation. For human females (whose young are dependent for very prolonged periods) the optimal mate would be a reliable long-term provider with genes for a healthy body and a strong immune system. For human males, two strategies for success are possible. Males can either be good long-term partners and providers (“dads”) or hit-and-run inseminators who aim to father children with as many women as possible (“cads”).

Across all human populations, females tend to value resource-providing ability in males, whereas males tend to value youth and beauty in females. Note that there are cultural differences in the type of female physique that men find attractive. This may change within a generation or two of changing society of residence, suggesting that it is not a genetically determined character, but within any given society is usually understandable in the context of the health of the prospective mate.

Facial attractiveness for both genders is focused on **symmetry** and “**averageness**”, both of which require a healthy immune system and genetic makeup. Men tend to find females with **infantile** faces (i.e. large forehead and eyes, small upturned nose, small chin) more attractive, perhaps because it elicits protective behaviour in males. Females tend to find males with physical evidence of high testosterone levels (e.g. large chin, tall and muscular frame, broad shoulders) more attractive. Since testosterone is an immune system suppressant, males with these features may be advertising that they have strong innate immune systems that can withstand high testosterone levels.

Returning to the “cads” vs “dads” strategy, “cads” tend to have physical features indicative of high **testosterone** levels. There is evidence that women find masculine-featured males more attractive when they are at the ovulation part of their menstrual cycle, and less masculine-featured males more attractive at other times. This may allow women to gain the “cad” genes for their offspring, while enjoying the benefits of “dad” reliability and support.

Mating systems in human societies

As inhabitants of modern western and eastern societies it is common for us to believe that fundamental aspects of our own societies reflect broader aspects of human culture, but at least with respect to mating systems, this is not the case. **Monogamy** (long-term pairing of one man and one woman), or at least “serial” monogamy, are the norm in modern society, but among pre-industrial “traditional” societies polygyny is/was the most common mating system. Societies which practice **polygyny** (where up to 20% of males have more than one female partner) account for more than half of human pre-industrial cultures. Polygyny/polygamy allows economically successful males to maximize their number of offspring, but can create significant problems, e.g. enforced marriage of women, crime among the males who do not find mates. Economists also note that successful males in polygamous societies tend to invest in their own children, rather than the infrastructure of the society.

Incest avoidance

Very close inbreeding (i.e. mating with one’s parent or sibling) has clear disadvantages, including loss of genetic variability and the increased likelihood of genetic diseases due to pairing of recessive alleles. Across all human societies, such first-order mating is very rare and usually is only tolerated for political purposes (i.e. strengthening dynasties as in ancient Egypt). Mating with first cousins also has some disadvantages, but these are not as severe as for first–order relative mating. Incest is mating with one’s close relative and is usually forbidden by taboos in most human societies. Often incest avoidance is implicitly forbidden, i.e. there may not be a written or spoken rule, but the practice is viewed as abhorrent. Note that incest taboos are not always based on genetics, for example mating between step-father and daughter may be regarded as incest, even though there is no genetic risk.

The **Westermarck contention** (or hypothesis) states that “siblings raised together for the initial 5 years of life develop an aversion to becoming sexual partners as adults”. This has been observed in studies of Israeli kibbutz children who, although genetically unrelated, have been brought up together almost as siblings and tend to avoid sexual relationships with each other. This phenomenon is probably an adaptation to avoiding incest and its adverse genetic outcomes.

Psychoactive substances

Use of psychoactive substances is widespread among most human societies. In fact many of our modern drugs of abuse (alcohol, cocaine, tobacco, marijuana) have been used at one stage by ancient societies. Psychoactive substances may be beneficial in traditional societies in that they relieve pain, act as stimulants, mobilize energy and facilitate social interaction.

Many psychoactive substances stimulate release of dopamine from pathways between the brainstem (ventral tegmental area) and the basal forebrain (nucleus accumbens). This pathway (mesolimbic dopaminergic pathway) is integral to the natural reward systems which drive our behaviour to seek food and comfort and therefore maximize Darwinian fitness. Genetically determined differences between individuals in the physiology of these reward systems probably underlies the different responses of individuals to drugs of abuse.

An example of a genetically determined difference in susceptibility to addiction concerns the ALDH2*2 allele. This is seen in east Asian people who have a very slow conversion of acetaldehyde to acetate. Accumulation of acetaldehyde after drinking alcohol leads to very unpleasant symptoms, making drinking of alcohol an aversive experience. Consequently, people with the ALDH2*2 allele have a greatly reduced susceptibility to alcoholism.

There are also genetic influences on the adverse effects of some psychoactive drugs. Early use of cannabis (before age 15) has been associated with an increased risk of schizophreniform illness (up to 10 fold risk, according to the Dunedin study, Caspi et al. 2005), but only in those with a genetic susceptibility. This genetic susceptibility may manifest through intrinsic differences in the way that the brains of susceptible individuals use the endogenous cannabinoid system (the endocannabinoid neurotransmitter anandamide).

Evolution and behavioural disease

All human societies have some individuals with behavioural (psychiatric) disease. In fact some diseases (e.g. **schizophrenia**) are encountered as frequently in traditional societies as they are in modern western society. Both schizophrenia and major depression are at least partly genetically determined, probably by the additive effects of multiple genes. Having one or both parents with schizophrenia increases the risk of developing the disease between 7.2 and 46.9 fold, depending on the study. Having one or more siblings with schizophrenia increases the risk of developing schizophrenia 7 fold.

Depression is a depression of mood and may be classified as major depression (lasting for more than 2 weeks) or minor depression (less than 2 weeks duration). Bipolar disorder is a fluctuation of mood between depression and abnormally elevated mood (hypomania).

Many of us experience minor depression at some stage during our lives, usually in response to adverse life events (death of a partner or a parent, divorce, loss of one's job). The behaviour associated with minor depressive episodes may be adaptive in that it attracts support from other group members and provides time for the individual to reassess goals and make new plans. Individuals who succumb to major depression may possess multiple copies of predisposing genes which individually are adaptive.

Schizophrenia is found in almost all cultures at rates of 0.5 to 1.0% and is characterized by delusions of self-reference (paranoia), auditory hallucinations, flattening of emotion, disorganized speech (word salad), and sometimes catatonic behaviour. Given the poor reproductive potential for individuals with schizophrenia, it is hard to understand why the genes predisposing to schizophrenia are maintained in the population. There may be a small reproductive advantage for the relatives of schizophrenics which maintains the predisposing genes in the human population. Relatives of schizophrenics often are more creative, may have better pain resistance, resistance to infection and may be able to use asocial traits to gain advantage from society.

Lecture 14 Origin and mechanics of bipedalism

Specific Objectives:

1. To consider current ideas concerning the reasons for the emergence of bipedalism in hominins.
2. To list the main skeletal, ligamentous and muscular features associated with bipedalism in hominins and be able to describe their functional significance.
3. To be able to discuss the biomechanical aspects of human walking, with particular emphasis on energy expenditure and efficiency.

Introduction

The defining feature of hominins is that they habitually walk upright. Note that the adoption of bipedal locomotion occurred early in human evolution and is apparent even in the earliest forms of 6 mya. It is not certain whether the earliest hominids had all the features of efficient bipedal locomotion, but important fossil finds like the Laetoli footprints and hominin foot bones indicate that even very early australopithecines were reasonably efficient bipedal walkers.

Why did our ancestors become bipedal walkers?

There have been many explanations advanced for this change. Not all of them could be said to be supported by evidence.

- Carrying of objects in the upper limb (tools, infants).
- Increased hunting efficiency because of the ability to carry tools; also walking upright is more energy efficient.
- Seed and nut gathering.
- Feeding from bushes in an upright posture.
- Visual surveillance for potential predators or other group members.
- Long distance walking is more efficient for a bipedal walker.
- Male provisioning of females with dependent offspring; this suggests the need to carry food, water, wood, etc.

Structural adaptations of bipedalism

There are many structural adaptations of the skeleton in the trunk and lower limb associated with bipedal locomotion. These include:

- **Skull balanced over the atlanto-occipital joint more evenly** than in apes. The foramen magnum and atlanto-occipital joint lie close to the middle of the skull in hominins. This minimizes the amount of muscular effort required to keep the skull upright.
- **Increased curvature of some parts of the spine**, particularly the lumbar (lower back) region. Lumbar vertebrae become thicker because they must support the weight of the entire trunk. The curvatures of the vertebral column permit the balancing of the upper trunk weight over the hips and lower limb. This also reduces the strain on back muscles and ligaments, thereby making long periods of upright walking and standing more energy efficient and comfortable.
- **Hip bone becomes shorter** and the **direction of pull of gluteal muscles changes**. The short hip bone of upright walkers allows a shorter and more stable line of transmission of the upper body weight to the hip joints. The muscles of the gluteal region (buttocks) are arranged differently in upright walkers. The largest muscle - gluteus maximus - has a line of pull directed more posteriorly in upright walkers than in apes. This allows the gluteus maximus to be a powerful extensor of the thigh for climbing stairs and running. Under the gluteus maximus lie the

gluteus medius and minimus muscles. The gluteus medius in particular is an important muscle for supporting the ipsilateral (same side) leg during the stance phase of the bipedal stride.

- **Increased relative length of the lower limb**, particularly the thigh. Everyone will have noticed that people with longer legs can travel faster and with less effort for a given pace. This is because the human stride depends on the lower limb acting as an inverted pendulum. The longer the pendulum the further the trunk moves with each stride.
- **Shaft of the femur (thigh bone) is angled in towards the knee**. This keeps the line of weight transmission from the upper body as close to the midline of the body as possible as the walker shifts from one leg to the other during striding.
- **Lower end of the femur becomes more ellipsoidal in shape** to facilitate locking of the knee in extension during prolonged standing. The knee joint of the modern human looks deceptively simple but is actually functionally complex. Humans are able to rotate the femur on the tibia at the end of extension (leg straightening). This stabilizes the knee for prolonged low effort standing. This function is assisted by the anterior cruciate ligament, which prevents excessive knee extension.
- **The foot develops an arch supported by strong plantar ligaments**. These ligaments help to store energy during striding. Metatarsals lengthen and toes shorten.
- **The big toe becomes adapted for "pushing off",** i.e. it is longer, parallel to the other toes, and rotated so that the pad faces the ground. Features of the Laetoli footprints (e.g. deep big toe impression and big toe nearly parallel with other toes) indicate that the hominins which made them had similar foot structure to modern humans.

Biomechanics of human walking

When humans walk each limb proceeds through sequential stance and swing phases. For much of each stance phase the lower limb behaves as an inverted pendulum, pivoting around the ankle joint. The swing phase involves the lifting of the limb off the ground and its forward movement in preparation for the next stance phase. This requires that the weight of the trunk be supported by the contralateral (opposite side) limb and this balancing depends on the gluteus medius and minimus muscles.

Biomechanical studies have shown that bipedal walking is less energetically costly than quadrupedalism, but note that bipedal *running* may be more costly than quadrupedal running. In fact, energy expenditure of bipedal walking per unit distance has a minimum value at 4 to 5 km/hr, the natural walking pace for humans. In the walking cycle there is an inverse relationship between gravitational potential and kinetic energy, i.e. while gravitational potential energy is increasing, kinetic energy is decreasing. In running, the curves of potential and kinetic energy are in phase, i.e. they increase and decrease together.

Lecture 15 Human sexuality and the problems of human childbirth

Specific Objectives:

1. To indicate differences (and similarities) between human sexuality and that of other primates.
2. To compare and contrast the relative sizes of the fetal head and maternal pelvis in several primates including humans.
3. To indicate the major dimensions and axes of the true pelvis in adult human females.
4. To indicate the major anatomical features of the human fetal skull.
5. To note the relationship between human female reproductive tract and the birth canal, and be able to discuss factors which turn the fetal head during movement down the birth canal.
6. To indicate biological and cultural human adaptations to the problem of getting a large fetal head through the pelvic cavity, including prolonged postnatal brain growth, moulding of the fetal head and assistance to the mother.

Introduction: How does human sexuality compare to that of other primates?

The sexual organs of all male primates are notable in that they are external (i.e. non-retractable) and significantly large in proportion to the size of the rest of the body. This applies to adult men as much as other primates.

The sexual behaviour of non-human primates is often strikingly different from that of humans. Chimpanzees, for example, are completely promiscuous. Females in heat (i.e. in oestrus) have the sexual skins of their buttocks highly swollen and brightly coloured. A female in oestrus will accept all interested males: Jane Goodall observed one female mating with 7 males within a short period, with no evidence of rivalry or sexual jealousy among the males. It is impossible to determine when the common human pattern of long-term bonding between males and females appeared, but this is probably associated with increased dependency of hominin infants, particularly as the brain enlarged.

As part of the secondary sexual characteristics of modern humans there is a specific distribution of adult body hair, most of which relates to the distribution of the apocrine sweat glands and pheromone production (armpit and pubic region). Also consider that, for a naked species, the pubic hair is often a contrasting colour to the skin and would act as a visual signal of sexual maturity for both sexes. We are no longer a naked species but we retain the original physical sexual signals. To compensate for covering our sexuality we dress in an obviously sexually dimorphic manner, except in business (e.g. the power suit of women). We even go to the trouble of covering our natural scents with artificial ones that are supposed to allure the opposite sex in the same manner as our original pheromones.

Contrast of the relative sizes of the fetal head and maternal pelvis in several primates including humans

Two of the structural adaptations important in human evolution, namely bipedal locomotion and large brain size, collide in the human female pelvis. In other words, the pelvic structural requirements of bipedal locomotion have to be accommodated at the same time as the birth canal is kept wide enough to allow the passage of a large-brained baby. Relative to the size of the maternal pelvis, human newborn infants have the largest head of any mammal.

The human female reproductive tract

The human reproductive system consists of: ovaries for egg production; a uterus for development of the fertilized egg to a term fetus; uterine tubes to convey sperm to the egg and to convey the fertilized egg to the uterus for implantation; and a vagina to receive semen and provide a passage for delivery of the term fetus.

The major dimensions and axes of the true pelvis in adult human females

The human pelvis consists of a true pelvic cavity, which contains the pelvic organs, and a false pelvis cavity above. The size and shape of the true pelvis is critical for successful passage of the fetus to the outside world. When viewed from above, most human female pelves are circular in outline. If the pelvis has a heart-shaped outline (as often seen in men's pelves) there may be serious problems with rotation of the fetal head during birth. When viewed in sagittal section, the birth canal initially is directed backwards towards the coccyx (tailbone). When the fetal head leaves the uterine cervix it must turn at 90^o to this initial direction, so that it can pass down the vaginal axis. This turning is critical because continuance in the initial direction can cause tearing of the posterior vaginal wall and even the anus. The fetal head also rotates as it moves down the birth canal as viewed from above. This rotation is able to take advantage of the largest dimension of the pelvis at successive levels of the true pelvis. Thus fetal heads are usually oriented transversely (cross-wise) at the upper aperture of the true pelvis (pelvic inlet), because that is the widest dimension at the pelvic inlet. As the fetal head descends it also rotates so that the back of the head faces obliquely in the mid-pelvic cavity, because that is the widest dimension at mid cavity. Finally the fetal head rotates so that the occiput (back of the head) is to the front when the fetal head emerges from the pelvic outlet, because the front-to-back dimension of the pelvis is the greatest at the outlet.

Major anatomical features of the human fetal skull

The head is the largest part of the human fetus, so its passage down the birth canal is the most difficult. Furthermore, the fetal skull usually leads the body during birth. The fetal skull consists of separate plates (frontal, parietal, occipital) with mobile sutures between. This gives rise to the anterior and posterior fontanelles, which can be felt at the junction between these plates in a new-born infant. The anterior fontanelle lies between the frontal and parietal bones, while the posterior fontanelle lies between the parietal and occipital bones.

If the head of the fetus is held erect, the distance between the nose and back of the skull is larger than if the skull is tilted with the neck flexed. Consequently fetal heads are flexed (i.e. chin on chest) during passage down the birth canal. This presents the quite small suboccipitobregmatic diameter to the birth canal. Fetal head flexion during early stages of movement down the birth canal also allows extension of the fetal head to be used to turn the fetal head into the vaginal axis (see below).

Factors which turn the fetal head during movement down the birth canal.

The fetal head must be rotated around the axis of the neck vertebrae, as well as extended under the pubic arch to enter the vaginal axis of the birth canal. A very important movement during birth is the change in direction from the uterine cervix axis of the birth canal to the vaginal axis of the birth canal. This is a change of about 90^o and is achieved by extension of the already flexed fetal head.

There are several structures in the mother's pelvis which help to direct these two types of movement (i.e. axial rotation and extension):

- The shape of the bony pelvis itself. The fetal head rotates to take advantage of the largest diameter of the maternal pelvis at each level.

- Sacrotuberous and sacrospinous ligaments assist the movement of the fetal head into the vaginal axis of the birth canal.
- Puborectalis muscle as a sling around the rectum and vagina – although less important than the ligamentous and bony factors.

Biological and cultural adaptations to the problem of getting a large fetal head through the pelvic cavity

This problem has been solved in a number of ways:

- Human term fetuses have brain sizes that are a smaller percentage of final adult size than other primates. This means more postnatal brain growth, greater neonatal dependency but enhanced opportunities for postnatal experience to affect brain development. Humans are said to be secondarily atricial. In other words they have only a single offspring per litter, but the infant is born immature.
- The human term fetal head moulds to the shape of the birth canal during parturition. This is achieved by virtue of mobile skull sutures allowing overlap of skull bony plates. The loose skull sutures also allow extensive brain enlargement after birth.
- The human female pelvis is wider than in males, with a broader subpubic angle to accommodate the fetal head during parturition.

Humans often have a great deal of assistance to the mother during delivery. This may be performed by relatives, friends or professionals (e.g. doulahs, midwives or obstetricians).

Lecture 16 The comparative anatomy and function of the hand

Specific Objectives:

1. To be able to indicate the main bones and muscle groups of the human hand.
2. To demonstrate the different types of hand movements, including pronation/supination, power grip, precision grip, opposition, divergence/convergence of the digits.
3. To describe the principal anatomical and functional differences between ape and human hands and describe the evidence for evolution of the hand in hominins.

The main bones and muscles of the human hand

The human hand consists of three groups of bones: carpals at the wrist, metacarpals forming the palm and phalanges in the fingers and thumb. The carpals articulate with the radius of the forearm at a joint which allows movement in two planes. The carpals are small bones of irregular shape, which fit together at plane joints. They form a tunnel called the carpal tunnel through which tendons, nerves and vessels destined for the hand must pass. The metacarpals make up the bulk of the hand and have condylar joints with the proximal phalanges at the base of the fingers. The phalanges come in three groups for the fingers (digits 2 to 5: proximal, middle and distal phalanges) or two for the thumb (digit 1: only proximal and distal phalanges). Muscles controlling the hand can be divided into extrinsics, which lie outside the hand in the forearm and act on the hand bones by means of long tendons, and intrinsics which lie within the hand itself. The intrinsic muscles lie in three main groups: one group at the base of the thumb (thenar muscles), one group at the base of the little finger (hypothenar muscles) and another group within the palm (interosseus and lumbricals).

Different types of hand movements, including pronation/supination, power grip, precision grip, opposition, divergence/convergence of the digits

The hand may be pronated and supinated (i.e. rotated around the axis of the forearm). This is important in tool use that requires rotational movement like using a screw driver or hand drill. Pronation/supination depends entirely on movement at joints near the elbow and at the wrist.

The power grip, as the name implies, is important for grasping a large object forcefully. A good example would be gripping a bat or club. One variant is the hook grip which we use for carrying objects e.g. briefcases. A power grip depends on force applied by the powerful forearm flexors, although the intrinsic muscles of the hand may contribute by shaping the fingers to the object.

The precision grip is used for fine movements involved in delicate operations, like threading a needle or writing. It depends mainly on actions of the intrinsic muscles of the hand. It may be further divided into translational (movement in one direction, e.g. threading a needle) or rotational movements (e.g. using a very small screw driver without forearm supination).

Opposition is an important hand movement which contributes to precision grip. It is present to a limited extent in many primates, but is best developed in the human hand, where the thumb pad can be brought into opposition with the finger pads of all the other digits.

Divergence and convergence of the fingers are present in many mammals with unspecialised forepaws and are most important in weight bearing on the forearm. In humans we use convergence in some specialised ways e.g. cupping the hand to hold water or in swimming strokes.

The principal anatomical and functional differences between ape and human hands and evidence for evolution of the hand in hominins

In all primates the forelimb is a versatile organ, but in humans the hand has particular features representing adaptations for enhanced tool use:

- Elongated thumb reaching almost to the first interphalangeal joint of the index finger.
- Rotated thumb to face across the palm, allowing improved opposability.
- Enhanced mobility of the thumb due to a saddle shaped first carpometacarpal joint, allowing the thumb to sweep across the palm during opposition.
- Enhanced development of the intrinsic muscles of the hand (at the base of the thumb and little finger) allowing opposition and precision translation movements of the fingers.

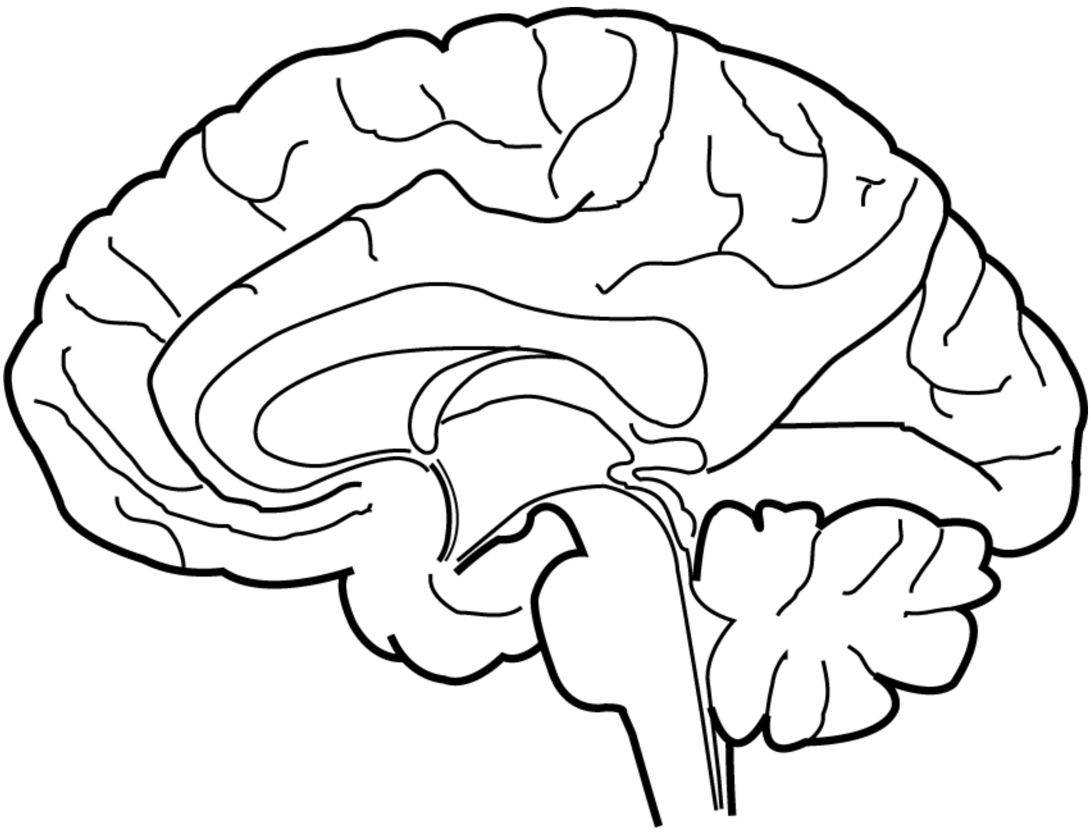
Hand bones from fossil hominins suggest that as early as 2 million years ago the hominin hand had many of the features of the modern human hand, but was not completely modern. For example the thumb length was elongated but intermediate between ape and modern human. This may have limited the ability of these early hominins to perform precision grip and thus restricted tool use.

Lecture 17 The hominin brain

Specific Objectives:
1. To be able to describe the main regions of the brain and indicate the broad function of each.
2. To describe the main functional areas of the cerebral cortex and indicate how they were discovered.
3. To be able to indicate the main stages in the increase in size of the hominin brain during evolution.
4. To define the term encephalization and indicate the relationship between body size and brain size.
5. To define functional cerebral asymmetry and consider its importance for hominin brain function.

Main brain regions

The brain can be divided into three basic regions: forebrain, midbrain and hindbrain. The forebrain consists of cerebral hemispheres which have a surface layer called the cerebral cortex, occupying about two-thirds of the weight of the human brain, and deeper structures like the thalamus and hypothalamus, which are concerned with sensory and motor relay function and control of automatic functions. The midbrain is very small and has visual reflex centres as well as bundles of axons passing between the cerebral hemispheres and the spinal cord. The hindbrain consists of medulla and pons, which have groups of nerve cells controlling breathing and the circulation and the cerebellum, which co-ordinates motor function.



Functional areas in the cerebral cortex

Beginning in the 19th century, studies of patients with brain injury to discrete parts of the brain have led to a good understanding of functional localization within the human cerebral cortex. In recent years these lesion studies have been supplemented and extended by electrophysiology, PET (positron emission tomography) scanning and functional magnetic resonance imaging (fMRI). We know of specific functional areas concerned with motor control (primary motor cortex and premotor cortex), perception of touch (primary somatosensory cortex), sound (primary auditory cortex), smell (primary olfactory cortex) and sight (primary visual cortex). Language areas have also been identified, but these will be dealt with in a subsequent lecture.

Stages in the increase in size of the hominin brain during evolution

The hominin brain has increased in size considerably (approximately three-fold) over the last 2 million years. Interestingly, the majority of this expansion has occurred well after the adoption of an upright stance. In fact increased brain size is used as the defining feature of genus *Homo*. But remember that brain size should be considered in relation to body mass - in other words, some of the expansion of the human brain is associated with larger body size. Nevertheless, most of the expansion occurring from *Homo erectus* on is probably associated with increasing cognitive ability. Note that modern *Homo sapiens* does not have the largest brain of any hominin. That honour belongs to some archaic *Homo sapiens* types (*Homo neandertalensis*).

Encephalization: the relationship between brain and body weight

Brains are concerned with sensing the outside world, deciding on appropriate actions and producing movement or action as a result of those decisions. The first and last of these functions mean that the brain is intimately connected with sensory receptors in the skin and must control muscles to produce actions. This means that if an animal has a larger body surface area or muscle mass, then brain weight also must be greater to cope with that mass. In other words, when we look across mammals, brain mass tends to increase with body mass, without any implication that the larger brained animal is "smarter". Nevertheless, some animals like humans have a much larger brain for their body weight than would be predicted by scaling up smaller mammals.

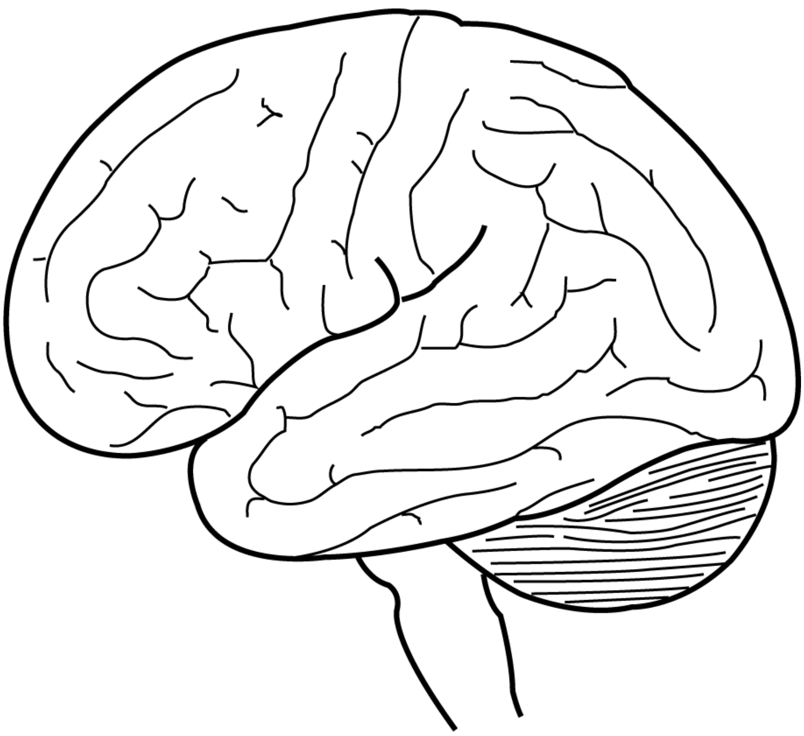
Encephalization is defined as increase in brain size beyond that which would be expected given the body size of a particular species. In the case of humans, this "extra" brain size can be used for so-called "higher functions" such as language, social function, sophisticated motor planning and enhanced spatial perception, as well as fine motor control.

Recent quantitative studies of mammalian and avian brains suggest that it is the number of constituent forebrain neurons that is the most significant determinant of cognitive function. Large brains may also be at a disadvantage compared to smaller brains because lines of communication between functional areas are longer in larger brains, so information transfer is slower. This means that small brains with high neuronal packing density and short distances between functional areas are best-equipped to be cognitively superior. This combination is seen in some birds (crows and parrots) and primates.

Asymmetry in the brain and cerebral dominance

As a result of "split-brain" experiments performed by Sperry and Gazzaniga it became apparent that some so-called "higher functions" such as language, music and spatial ability may be concentrated in one side of the human brain. This is possible because a large fibre bundle called the corpus callosum joins the two hemispheres, permitting rapid transfer of information between the two hemispheres. The localization of particular functions on one side of the brain may have been an advantage for hominins in that it allowed more efficient use of the available brain tissue. In other words - why have two different regions on opposite sides of the brain performing the same function, when one area would do? Why not use the other side for a different but related function (e.g. music as opposed to language)?

Anatomical asymmetry is not the sole province of humans. Many ape brains show anatomical asymmetry particularly in the length and shape of the lateral fissure, a groove which separates the frontal and temporal lobes. The significance of this is that special language areas are located on the upper bank of (usually) the left lateral fissure. Endocranial casts of fossil hominins also show anatomical asymmetry. Enhanced impressions of frontal or occipital poles of the brain on one side are found in Neanderthals and are known as petalias.



The metabolic cost of the large neuron-rich human brain

Brain tissue is metabolically expensive. This metabolic cost is mainly determined by the number of neurons, i.e. the more neurons the higher the metabolic cost. The brain of modern humans contains about 86 billion neurons (nerve cells), compared with 35 billion for the orangutan, 33 billion for gorillas and 28 billion for chimpanzees. The modern human brain weighs only 2% of the human body, but consumes about 528 kCal per day, about 20% of the daily energy requirements of humans. Contrast this with orangutans who use only about 10% of their energy intake to run their smaller brains. This metabolic cost demands quality sources of high energy, such as would have been provided by eating meat and cooking of vegetable foods. So brain expansion goes hand-in-hand with behavioural adaptations that have improved the diet of our ancestors.

Lecture 18 Language, speech and the human face

Specific Objectives:

1. To discuss the elements of language and contrast human language with animal communication.
2. To discuss the significance of language areas in the brain and the pathway between them.
3. To be able to describe the main structural features of the human pharynx, larynx, tongue, palate, nasal cavity and oral cavity.
4. To be able to indicate how the sound of the human voice is produced by vibration of vocal folds.
5. To be able to discuss the production of vowels and consonants by dynamic adjustment of the column of air above the larynx.
6. To be able to summarize the similarities and differences between the modern human vocal apparatus and that in apes and ancient humans.
7. To be able to summarize key findings concerning language capabilities in apes.
8. To be able to indicate the importance of the human face in communication and recognition of individuals.
9. To describe the major facial muscles and indicate the regions of the cerebral cortex concerned with motor control of the face and processing sensory information from the face.
10. To indicate the nerve pathways involved in control of the facial expression muscles.
11. To indicate the regions of the brain concerned with vision and the sensory information pathways concerned with the recognition of human facial features.

What is language?

Language is the ability to encode ideas into signals for communication to someone else. It should be distinguished from thinking which is the ability to have ideas and infer new ideas from old ones. People do not think only in the words and sentences of their own language. It is possible for infants, non-human primates, aphasic patients and normal adults to think using visual images, abstract concepts and propositions. Language should also be distinguished from reading and writing. Written language is a recent invention in human history and must be explicitly taught, whereas language skills appear to be (at least in part) intrinsic to the modern human brain.

Language has a universal design

Language is based on two components: words and grammar. **Words** are arbitrary associations between a sound and a meaning. By age 6, children comprehend about 13,000 words and a high school graduate should have mastered at least 60,000. This means that children connect a new sound and meaning about every 90 waking minutes. **Grammar** is the system that specifies how vocabulary units can be combined into words, phrases, and sentences and how the meaning of a combination can be determined by the meanings of the units and the way they are arranged.

Grammar has three main components: morphology, syntax and phonology. **Morphology** refers to the rules for combining words and affixes into larger words. This is very important in languages like Latin, old English and ancient Greek, where affixes convey much of the meaning of who did what to whom, but not so significant in modern English. **Syntax** consists of rules for combining words into phrases and sentences and determining relations between words. If a language has lax rules about morphology than syntax becomes more important in conveying meaning (e.g. modern English). **Phonology** consists of rules for combining sounds into a consistent pattern for the language. For example, some words sound like they could be English words while some do not. Phonology also includes prosody, which is the patterns of intonation, stress and timing that span entire phrases and sentences. Prosody can have a grammatical role (e.g. in distinguishing "black board" from "blackboard") or serve a broader function in distinguishing questions from statements, supplying emphasis, indicating sarcasm and expressing emotion.

Communication among animals

The natural communication systems of non-human animals are very different from human language. They are based on one of three designs: a finite repertoire of calls, with each call having a specific meaning, a continuous analog signal that registers the magnitude of some condition (e.g. bee dances) or sequences of randomly ordered responses that serve as variations on a theme (e.g. birdsong).

The antiquity of human language: Is language innate?

It is impossible to know precisely when human language first appeared. It appears likely, from the complexity of the cultures of upper paleolithic people, that they possessed complex spoken language. Certainly all modern humans possess language, suggesting that language in anatomically modern humans is at least 50,000 years old (the point at which modern humans diverged from each other). Contrast this with writing which is only 5,000 years old or less.

Although language must be learned, several lines of evidence suggest that the ability to learn language is innate. In 1959, Noam Chomsky proposed that children possess innate neural circuitry specifically dedicated to the acquisition of language. People in technologically primitive cultures, helpless 3 year olds, and poorly educated adults in our culture all master complex grammar when they first acquire language, and they do so without special training sequences of feedback. When children in a social environment are deprived of a bona fide language, they create one of their own (e.g. sign language of the deaf). In the eighteenth and nineteenth centuries, slave children living on plantations developed full-fledged languages (*creoles*) from the crude pidgin languages (choppy strings of words) spoken by their parents. Note that language and general intelligence can be dissociated from each other in several pathological conditions. In other words some individuals can have normal or high intelligence but very poor language ability while some mentally retarded individuals (e.g. Williams syndrome) can have quite fluent language.

Everyone recognises the difficulty of learning a new language when we are older, whereas young children acquire language apparently by osmosis. Noam Chomsky recognised that children aged between 6 months and 4 years rapidly acquire the language they hear spoken around them without any instruction in grammar and minimal correction of pronunciation. This ability is universal for all human populations and so similar in nature across the world that it appears to be programmed into our genes. The ability to acquire language declines markedly after the age of 8 and is particularly difficult after 16 years. Familiarity is critically important to the retention of skills in a particular language. Exposing children from an English speaking background to Chinese sounds during babyhood (9 months of age) greatly improves their ability to understand Chinese and retain Chinese language skills into older life.

Structural features of the human pharynx, larynx, tongue, palate, nasal cavity and oral cavity

The larynx and lower respiratory tract develop from the gut during embryonic life. Consequently, sound from the larynx must pass up through the pharynx, oral cavity and sometimes the nose to produce speech. The nasal and oral cavities are separated by the palate (with hard and soft parts).

Production of the human voice by vibration of vocal folds

The human larynx consists of a "skeleton" of cartilage covered by muscles and mucous membranes. The most important feature of the larynx is the paired vocal folds. These are formed by the upper edges of a tent-like membrane and are covered by mucous membrane. When the vocal folds are pressed together and air from the lung is forced past them, the vocal folds vibrate. The length, tension and mass of the vocal folds can be adjusted to alter the pitch of the sound produced.

Vowels and consonants

The sound produced by vibration of the vocal folds passes up into the pharynx, oral cavity and nasal cavity. Adjustment of the shape of this column of air above the vocal folds leads to the production of vowels.

Consonants are aperiodic noise introduced into the "pure" sound of vowels. This is achieved by sudden and transient obstruction of the column of air above the larynx. Consonants may be named according to the site at which they are produced (e.g. labial consonants like "b" and "p" or dental consonants like "d" and "t").

Language areas in the brain

During the late nineteenth century, careful analysis of the brains of individuals who had suffered localized brain damage allowed neurologists like Broca and Wernicke to determine that there are specialized regions of the brain concerned with language. In both right and left-handed people these areas are mainly located in the left cerebral hemisphere, but about 15% of lefties have their language areas in the right hemisphere. **Wernicke's area** is concerned with the comprehension of speech. **Broca's area** is concerned with expressive aspects of language. A prominent fibre bundle called the **arcuate fasciculus** joins the two, thereby allowing the continuous feedback from Wernicke's to Broca's areas to monitor an individual's speech. Other areas are concerned with comprehension of written language (**visuolexic region**).

This description of language areas is known as the **Wernicke-Geschwind model**. Note that the Wernicke-Geschwind model has some limitations. Firstly, the arcuate fasciculus is bidirectional not unidirectional, joining a broad expanse of sensory cortices with prefrontal and premotor cortex. Secondly the roles of Broca's and Wernicke's areas may not be as clear-cut as at first thought. Thirdly, a variety of regions in the left hemisphere (both cortical and subcortical) appear to be critically involved in language processing. These include higher order association cortices in the left frontal, temporal and parietal lobes which seem to be responsible for mediating between concepts and language; selected tissue in the left insula cortex involved in articulation, and prefrontal and cingulate cortex involved in memory associated with language.

A modern view of language neurology proposes that there are three brain systems involved in language. The **language implementation system** includes Broca's and Wernicke's areas and the arcuate fasciculus, selected areas of the insula and the basal ganglia. The implementation system analyzes incoming auditory signals so as to activate conceptual knowledge and also makes sure that phonemic, grammatical construction and articulatory control are maintained. The second system is the **mediational system**, which consists of numerous regions in the temporal, parietal and frontal association cortices. The mediational system acts as a broker or intermediary between the implementation system and the third system – **the conceptual system**, which is a group of areas distributed throughout the remainder of the higher order association cortices, which together support conceptual knowledge.

Note that rapid human speech is also a feat of muscular co-ordination in that long sequences of vowels and consonants require rapid switching of activation from one group of laryngeal, oral and palatine muscles to another. This requires good motor cortex and cerebellar function as well.

Note that rapid human speech is also a feat of muscular co-ordination in that long sequences of vowels and consonants require rapid switching of activation from one group of laryngeal, oral and palatine muscles to another.

Similarities and differences between the modern human vocal apparatus and that in apes and ancient humans

The vocal tract in apes, as seen in sagittal section, has a proportionately shorter vertical height than in adult modern *H. sapiens*. A short vocal tract is also present in infant modern *H. sapiens*. Certainly, apes appear to be unable to produce the complex range of sounds produced by modern humans, although ape capacity for symbolic behaviour appears surprisingly good (see below). Some authors have claimed that Neandertals were incapable of human speech (on the basis of the estimated height of the vocal tract), but the current consensus is that they were capable of articulate speech. Recently analyses of the **hypoglossal canal**, which transmits the hypoglossal nerve for control of the tongue, in Neandertal fossils, suggests that Neandertals and other archaic *H. sapiens* had hypoglossal canals as large as those in modern humans. On the other hand, the same authors concluded that apes, australopithecines and early *Homo* had small hypoglossal canals. Note, however, that this last contention has been disputed by later studies. Furthermore, hypoglossal canal size may not always correlate accurately with size of the nerve.

Language capabilities in apes

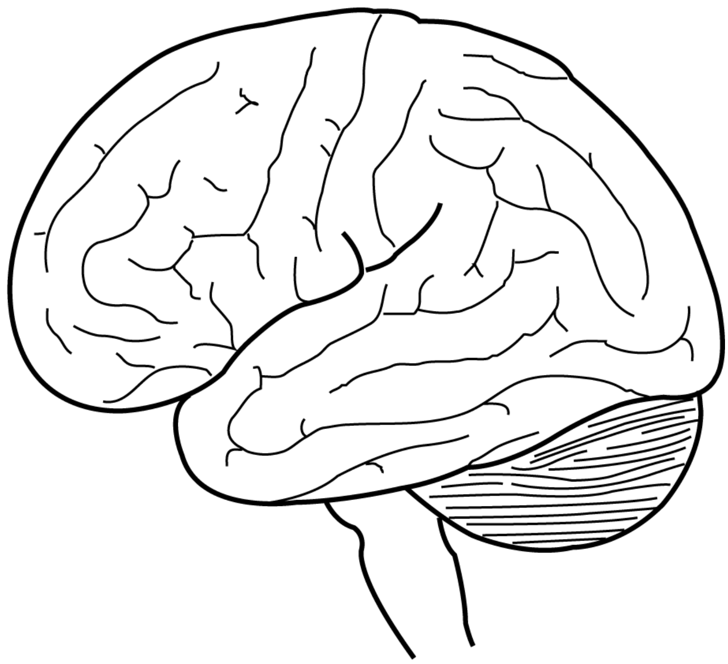
Apes do not have the sort of vocal apparatus that permits spoken language, but it was realized in the last few decades that this does not preclude their use of symbols to convey meaning. In fact apes show cerebral asymmetry (see previous lecture) and may well have language-related structures in the brain. In 1966, Beatrice and Allen Gardner began to teach American Sign Language (ASL) to an infant female chimp named **Washoe**. In just over three years Washoe acquired at least 132 signs. She was able to ask for goods and services and also asked questions about the world of objects and events around her. When another young chimp (Loulis) was placed in Washoe's care, she actively taught Loulis some signs. Experiments like this indicate that apes are capable of using symbols to refer to concepts, other people and objects, even if the symbol bears no resemblance to the object itself. This implies some degree of **symbolic thought**.

Further studies showed that when apes were taught a symbol for food they were able to **categorize** unfamiliar items (e.g. new types of food) within familiar symbols. This suggests that they do understand the representational value of symbols. It is quite likely that the last common ancestor that apes and hominins shared also possessed communication capabilities similar to those we now see in African great apes. In discussions of evolution of the human brain much emphasis is usually placed on the increase in size, but equally important is the issue of

reorganisation of cortical functional areas and the connections between them. This reorganization allows enhanced functions to emerge from existing brain size.

The human face in communication and recognition of individuals

The human face is important in conveying emotions and this is an important aspect of human communication. Human faces are also distinctive and we have the ability to recognize subtle differences between the appearance of faces of individuals (e.g. police "Identikit" pictures). This allows ready identification of important and/or familiar individuals in human social groups.



The major facial muscles

Muscles concerned with altering the appearance of the face usually have attachments to the facial bones on the one hand and the deep connective tissue of the face on the other. The largest muscles encircle the orbits and the oral cavity. Around the orbit and extending into the eyelids is a muscle known as the **orbicularis oculi**, which is concerned with closing the eyes tightly. Similarly, the mouth is encircled by the **orbicularis oris**, which is important in pursing the lips for whistling, kissing, sucking, drinking from a cup and expressing disapproval. The side of the mouth is formed by a muscle called the **buccinator**, which inserts into the orbicularis oris. The buccinator provides tone and strength to the side of the mouth and assists with the movement of food onto the molar surfaces during chewing. On the forehead lies a muscle called the **frontalis**. This muscle inserts into a fibrous sheet (**galea aponeurotica**) which carries the scalp skin and hair. Another muscle at the back of the head (occipitalis) attaches to the back of the galea. The frontalis and occipitalis are able to move the scalp backwards and forwards, while the frontalis alone can elevate the eyebrows and wrinkle the forehead skin (e.g. in surprise). Many small muscles are located around the mouth and lower nose. The **levator anguli oris** pulls the side of the mouth upwards, the **depressor anguli oris** lowers the side of the mouth, while the **risorius** pulls the sides of the mouth backwards in a sneer or grimace. Muscles also elevate the side of the fleshy nose.

Regions of the cerebral cortex and nerve pathways concerned with motor aspects of facial function

Motor control of the face originates in the cerebral cortex in premotor cortex and the primary motor cortex. As we have already seen, the primary motor cortex has large areal representations for the face, indicating the behavioural importance of fine motor control of this region. In the pons lies the facial motor nucleus, which contains motor nerve cells which directly drive the facial muscles. The motor cortex sends messages to the facial nucleus by corticobulbar axons. These come from the opposite side of the cerebral cortex for motor cells driving muscle below the eye and bilaterally for motor cells driving muscles in the upper third of the face. Note that facial muscles can be under voluntary control by the cerebral cortex or non-conscious control by brainstem centres in the event of emotional responses. In other words, a smile can be warm and genuine, or a calculating pretence. The facial muscles are controlled by the facial nerve, which emerges from the skull behind the ear, passes through the parotid salivary gland, and ramifies across the face.

Regions of the cerebral cortex and nerve pathways concerned with sensory aspects of facial function

The primary somatosensory cortex has a large area devoted to representation of the face, and in particular the lips. Information for the somatosensory cortex is conveyed from the skin surface by the trigeminal nerve, which has three branches serving the forehead, cheek and jaw, respectively. Within the brainstem, information is processed by the trigeminal sensory nuclei and conveyed to the thalamus before being directed to the primary somatosensory cortex.

Regions of the brain concerned with vision and the sensory information pathways concerned with the recognition of human facial features

The primary visual cortex in the occipital lobe is the part of the cortex that is concerned with initial analysis of visual information. From here visual information is channeled either towards the posterior parietal lobe (dorsal stream) for analysis of location of visual features or down into the inferior temporal lobe (ventral stream) for recognition of form (including facial features).

Lecture 19 Variation and adaptation of modern humans

Specific Objectives:

1. To describe modern clinal and multivariate interpretations of human population diversity, indicating the limitations associated with older typological approaches such as racial classification.
2. To be able to discuss genetic variation within human populations, indicating which proportion is due to individual variation within groups and which is due to differences between groups.
3. To distinguish between adaptation and acclimatisation as applied to human populations.
4. To explain how environmental factors (solar radiation, temperature and altitude) influence human variation, using examples from each category.

Human population diversity

All modern humans are members of a **polytypic** species. A polytypic species is one which is composed of local populations which differ with regard to the expression of one or more traits. In discussions of human variation, people have usually lumped together various attributes such as skin colour, facial shape, hair colour and form (curly or straight), and eye colour. People possessing particular combinations of these traits have been placed together in categories associated with specific geographical locations. These categories have been called **races**. Some anthropologists today recognise population patterning corresponding to three major racial groups with each composed of several sub-groupings.

While **typological** concepts such as race may be useful in certain areas of anthropology (e.g. forensic anthropology where identification of the racial group of a skeleton can assist police), there are major problems with such an approach to human variation.

- Characteristics that have been traditionally used to define race are polygenic, and exhibit a continuous range of expression. This means that it is difficult to draw distinct boundaries between populations with respect to many traits.
- Which traits should be used to classify races? In any population there will be individuals of one so-called racial group, as judged by one trait, who fall into the normal range of another group as judged by another trait.
- Racial classification of individuals is often subjective.
- Racial classifications have in the past (and occasionally today!) been used to justify racist beliefs and persecution.

Genetic variation within human populations: variation within groups vs differences between groups

By the 1960's studies of individual polymorphic traits (allele variants of a single gene) were used as an alternative racial approach. These show continuous distribution of allele frequencies over geographic space (**clinal distribution**) and were useful to show microevolutionary changes from natural selection and gene flow due to population movements. Even clinal distribution analysis has its drawbacks in that there are many traits which make up human diversity. More modern techniques use a **multivariate analysis** involving dozens of gene frequencies. An example is Lewontin's 1972 study of 17 polymorphic traits. Lewontin calculated that only 6.3% of the total genetic variation among humans is explained by differences among major populations (7 groups: Caucasians, Black Africans, Asians, South Asians, Native Americans, Oceanians, Australians). In other words, close to 94% of human genetic diversity occurs within the geographical clusters. The larger population subdivisions within the geographical clusters (e.g. within Caucasians: Arabs, Basques, Welsh) account for another 8.3%. This means that geographical and "local" races together account for only 15% of all human genetic variation.

Cavalli-Sforza and colleagues (1988) later evaluated 44 different polymorphic traits in 42 different human sample populations. From these findings they constructed a dendrogram representing relationships between populations. Their findings have also been supported by mitochondrial DNA analysis. Africans appear to be genetically distant from all other human groups and within Africans there is more genetic diversity than among all other population groups. Two major groups emerge among all other humans. One group comprises New Guinean, Australian, Pacific Islander and Southeast Asian; the other is made up of Asian, Native American, European and non-European Caucasian. These findings hint at ancient migrations of modern humans.

Note that among the polygenic traits of humans one may include intelligence. The finding that most genetic diversity is within population groups indicates that claims that particular racial groups are genetically inferior with respect to intelligence have no scientific basis.

Adaptation and acclimatisation among humans

Like all other mammals, humans show particular biological adaptations to the environment in which they live. **Adaptation** is defined as a long-term evolutionary (i.e. genetic) change in a population occurring as a functional response to environmental conditions. It should not be confused with **acclimatisation**, which is a physiological response to changes in the environment that occur during an individual's lifetime. Acclimatisation is often short-term (e.g. tanning) and is not a genetic change itself. Note however that the *capacity* for acclimatisation is under genetic influence.

Environmental factors (solar radiation, temperature and altitude) influencing human variation

There are many interactions between human genetic variation and the environment. We will consider 3 examples:

i) Solar radiation, skin colour and vitamin D

Skin colour is another example of adaptation in human populations. Obviously populations with the greatest amount of skin pigmentation are found in the tropics, with lighter skin colour associated with more northern latitudes. Skin colour is influenced by three substances: **hemoglobin**, **carotene** and **melanin**. Melanin is the most important and is produced by specialized cells in the skin called melanocytes. All humans appear to have the same number of melanocytes; it is the amount of melanin per cell and the granule size which varies. Melanin absorbs potentially dangerous UV radiation and provides protection from excessive UV exposure which can cause genetic mutations in skin cells leading to skin cancer.

Early hominins lived in equatorial areas, so it is likely that these ancestors had high levels of melanin production. However, once our ancestors migrated out of Africa other selection pressures would have come into effect. As they entered Europe for example, where cloudy skies and short winter days meant reduced levels of UV radiation, the selection pressure for melanin production would have diminished and another factor would have come into play - vitamin D. **Vitamin D** plays a vital role in the mineralisation and normal growth of bone during infancy and childhood and is available in only a few foods such as fish oils, egg yolk, butter, cream and liver. The body's principal source of vitamin D is through synthesis in the skin by the interaction of UV light and a cholesterol-like substance in skin cells. Failure to obtain sufficient vitamin D leads to rickets, which gives rise to bone deformities, especially the weight-bearing bones of the lower limb and pelvis. Pelvic deformities are a particular concern for women, because they can lead to a narrowing of the birth canal, which in the absence of surgery will lead to the death of both mother and fetus during birth. Thus, in areas of the world where UV exposure is reduced, there is actually a selection pressure towards lighter skin.

ii) Temperature

Adaptations to heat: Early hominins evolved in hot environments and this explains why humans cope better with higher rather than lower temperatures. **Sweat glands** are distributed throughout the skin and sweat makes possible the dissipation of heat by evaporation. The number of sweat glands in an individual is about 1.6 million and is fairly constant in all human populations. Another mechanism for heat dissipation is **vasodilation**, whereby vessels near the skin dilate to permit increased blood flow to the skin. Body size and proportions are also important in body temperature regulation (see below).

Adaptations to cold: Humans can respond to cold by either increased heat production or reduced loss. The latter is preferable because energy is derived from dietary sources and unless food supplies are abundant, prolonged increased energy production is difficult. In cold environments humans respond by increasing basal metabolic rate, shivering, and vasoconstriction. Inuit (Eskimo) people living in the Arctic maintain metabolic rates between 13 and 45% higher than non-Inuit controls. The highest metabolic rates have been seen in inland Inuit. Vasoconstriction reduces blood flow to the skin and hence heat loss, but prolonged vasoconstriction can be hazardous, because prolonged vasoconstriction can cause frostbite if the ambient temperature is below 0^{o}C. Central Australian aborigines show prolonged vasoconstriction of their feet during sleep, because the air temperature does not fall below freezing, but in Inuits there is intermittent vasoconstriction alternated with periods of vasodilation. This compromise allows periodic warming of the skin to prevent frostbite.

Two rules concerning body shape and proportions in response to temperature:

Bergmann's rule concerns the relationship of body mass or volume to surface area. Body size tends to be greater in colder climates. This is because as mass increases, the ratio of surface area over body mass decreases, thereby allowing reduced heat loss.

Allen's rule concerns body shape, especially appendages. In colder climates, shorter appendages, with increased mass to surface area ratio are adaptive because heat loss is minimized. Conversely longer appendages, with increased surface area to mass ratio, are adaptive in warmer climates in that they facilitate heat loss.

iii) High altitude

At high altitudes there are several stressors: reduced available oxygen (**hypoxia**), more intense solar radiation, cold, low humidity, wind, reduced nutritional base, lower iodine and rough terrain. Changes to the fat distribution in the upper eyelid are adaptive to extremes of glare and wind and produce the typical appearance of the Asian eye. Hypoxia results from reduced barometric pressure and has severe impacts on reproductive success. In particular, recent immigrants show increased infant mortality, increased risk of miscarriage, prematurity and low birth weight. These appear to be due to impaired maternal-fetal transport of oxygen. There is evidence that some populations have become genetically adapted to high altitudes. For example, indigenous peoples of Tibet who have inhabited regions higher than 4,000 metres for 25,000 years have birth weights as high as those from lowland Tibetan groups and higher than those of recent Chinese immigrants. In other studies it has been shown that highland Tibetans and the Quechua (inhabitants of highland Andes) burn glucose in a way that permits more efficient use of oxygen. This implies genetic mutations in mitochondrial DNA that direct glucose metabolism.

Lecture 20 Changing patterns of disease during human history

Specific Objectives:

1. To be able to define the terms paleopathology and pseudopaleopathology.
2. To be able to indicate how changes in human society, from hunter-gatherer to modern industrialised society, have influenced disease patterns in human populations.

Paleopathology and Pseudopaleopathology

Human **paleopathology** is defined as the study of disease in ancient populations by the examination of human remains. True paleopathological changes in human remains need to be distinguished from **pseudopaleopathology**, which is defined as structural change in normal soft tissue or bone that resemble a lesion of some ante-mortem (before death) disease, but is in fact the product of a postmortem process. Examples of pseudopaleopathological changes include:

- Mortuary practices – i.e. actions of individuals preparing the body after death
- Postmortem changes due to action of body's own intestinal flora
- Postmortem changes due to action of insects (larvae of flies) and scavengers
- Excavation artifacts (damage from excavation tools or subsequent handling and transport)
- Botanical effects (plant roots may penetrate orifices and fracture bone postmortem)
- Chemical erosion (e.g. bone mineral extraction by wet acidic soil causing resemblance to osteporosis)
- Effects of temperature changes (freeze-thaw conditions may shatter buried bone)

Changes in human societies and its effect on patterns of disease

For the purposes of understanding changes in human disease during prehistory and history it is useful to divide the human disease story into 5 stages:

- Paleolithic and mesolithic cultures (hunter –gatherer society)
- Early agricultural societies (neolithic)
- Copper, bronze and iron ages: early trade routes
- Ages of discovery and colonialism
- The global culture

Hunter-gatherer societies consist of groups of usually 25 people and certainly no more than 50 living in comparative isolation from other groups. Under these circumstances, infectious diseases which require transmission from one individual to another at the height of pathogen load are unlikely to be able to spread to sufficient new hosts to achieve an epidemic or even maintain an endemic presence. This means that many of the infectious diseases that are common in settled human communities (e.g. measles, mumps, rubella, influenza) are unknown or very rare among hunter-gatherers. Major causes of morbidity and mortality among hunter-gatherers are trauma, childbirth, nutritional disorders, infections and parasitic infestations from the natural environment.

When humans began to adopt a settled existence with overall higher population density and larger population groups, infectious disease could more readily spread throughout the population. This leads to the emergence of new infectious diseases, possibly transferred from the natural environment or mutated from relatively harmless microorganisms already living as human commensals. So settled life brings with it epidemics of viral diseases (measles, mumps, rubella, influenza), poor water supply and proximity of faecal matter to water sources promotes intestinal infections and infestations (cholera, amoebiasis, hepatitis), and close proximity in crowded housing promotes spread of pulmonary infections (tuberculosis). Note that some human groups were isolated from the bulk of the human population during the transition from hunter-gather society to settled existence (e.g. native Americans, indigenous Australians, Polynesians). This means that prior to the spread of old world humans during the 15th and subsequent centuries, isolated human populations either had their own specific infectious diseases or enjoyed relative protection from infectious disease as part of their isolation. This obviously changed with contact between old and new world humans. Another important point about settled existence is that changes in diet from hunter-gatherer to agricultural may significantly affect the incidence of nutritional and dental disease in humans. A good example of this is illustrated by enforced aggregation of Native American people in Florida into Spanish missions with sole reliance on maize for food. This led to profound health effects because maize is a poor source of many essential amino acids.

Trade routes facilitate the spread of disease, as seen with the spread of bubonic plague from central Asia to East Asia and Europe during the 14th century. Industrialized transport brought its own hazards by facilitating the spread of cholera from its original site in the Ganges river system to waterways of almost all parts of the world.

Smallpox is an acute, febrile illness of humans caused by the variola virus and characterized by a vesicular skin eruption. Its severe form is fatal in 25 to 40% of cases. The disease is unique in that it has no known animal or extracorporeal reservoir. Only humans contract smallpox naturally and all transmission is therefore human-to-human. Smallpox can only be perpetuated in large, densely populated concentrations of humans as are found in large cities. Not surprisingly then, there are no indications of smallpox in prehistory. The earliest historical descriptions of smallpox pertain to Egypt in the 6th century AD. Smallpox was not a significant disease in Europe until 1500 AD, reaching Denmark by 1300, Iceland by 1400 and Greenland by 1700. Smallpox was clearly absent from the pre-Columbian Americas. Smallpox reached Hispaniola in 1518 and resulted in the virtual extinction of the aboriginal population. In 1520, smallpox reached the Aztec empire and caused a 50% mortality within a few years. Indeed, it has been estimated that a pre-Cortes population of 25 million in central America declined to 2.5 million by 1608. Similarly, the Andean region (including the Inca Empire) is believed to have suffered 90% case mortality due to smallpox.

Ebola

Ebola is thought to have arisen from bat populations in the Democratic Republic of Congo (Ebola river region). It is introduced into the human population through close contact with the blood, organs or other bodily fluids of infected animals. This may be microbats or other infected mammals, such as chimpanzees, gorillas, fruit bats, monkeys, forest antelope and porcupines found ill or dead or hunted in the rainforest.

Once it is within a human population, Ebola can then spread through human-to-human transmission via direct contact (broken skin or mucous membranes) with the blood, secretions, organs or other bodily fluids of infected people, and with surfaces and materials (e.g. bedding, clothing) contaminated with these fluids. Humans are not infectious until they develop symptoms. Incubation period is 21 days. Symptoms include fatigue, muscle pain, sore throat, headache, followed by vomiting and diarrhoea, rash, signs of liver and kidney failure, and most importantly internal and external bleeding. Mortality rate is often 50%.

Lecture 19a Food and Diet

Specific Objectives:

1. To consider the evolution of human nutritional requirements and how this influences the health of modern humans and the incidence of so-called “diseases of civilisation”.

Human nutritional requirements and local food availability

Humans have inherited the ability to digest and process animal protein because the first mammals and primates were insect eaters. Early primates also evolved the ability to process most vegetable material. Our more immediate ancestors were primarily fruit-eaters, so we are able to process fruits. Thus the omnivorous nature of hominins reflects successive stages of primate evolution.

Human needs for specific vitamins and minerals reflect these ancestral nutritional adaptations. For example, **vitamin C** (ascorbic acid) is a crucial compound for all animals, so crucial that many animals are able to manufacture it. However, early monkeys received so much vitamin C in their diets of fruits and leaves, that the ability to manufacture vitamin C was lost. During pre-agricultural times the average daily intake of vitamin C was 440 mg, compared to approximately 90 mg in the average modern western diet. Insufficient vitamin C leads to scurvy (gum bleeding, slow wound healing, anemia and abnormal bone formation).

Humans also lack the ability to synthesize some of the amino acids (the **essential amino acids** - eight for adults, nine for infants). Interestingly, the amounts of each of the amino acids we need parallel the amounts present in animal protein, suggesting that food from animal sources may have been an important component of ancestral hominin diets when our specific nutritional requirements were evolving. In modern times, when meat consumption is both ecologically and economically expensive, the essential amino acids can be obtained by combining legumes and grains.

Pre-agricultural diets were high in animal protein, low in saturated fats, high in complex carbohydrates, low in salt and high in calcium. The modern western diet is almost the opposite configuration to this!! There is very good evidence that many of today’s diseases in industrialised countries are related to the lack of fit between our diet today and the one with which we evolved.

Our ancestors developed the ability to store excessive dietary energy as fat. This was an advantage in the past when food availability often alternated between abundance and scarcity (feast or famine). However, today people spend their lives with relative abundance of food. Obesity is now associated with many health problems, so our ability to store fat is a liability in an environment of constant feasting.

As humans spread into many ecosystems around the world, where local plant and animal foods, poisons and medicines vary considerably, a close fit has evolved in each population between nutritional availability, dietary preference and other ecological factors. Migration and cultural change (often forced) can produce a mismatch between local adaptations and a new diet and lifestyle with profound health implications. These include the so-called, syndrome X, comprising adult onset diabetes, obesity, and heart disease.

Cultural needs can put selection pressure on taste preferences and food tolerances with a profound effect on local diets. This is reflected in population preferences for chilies and highly spiced foods. In other populations with a history of heavy reliance on farming and agriculture, the normal states of lactose and alcohol intolerance have been reversed.

Lecture 21 Syphilis, Tuberculosis and HIV/AIDS

Specific Objectives:

1. To be able to describe the 4 main types of treponemal infection and indicate how they represent adaptation of treponemes to exploiting the environment of the human body in different climates.
2. To describe how syphilis influenced human culture.
3. To be able to describe the basic pathogenesis of tuberculosis and its history in human populations.
4. To be able to discuss the concept of evolution and adaptation in a pathogen using HIV as an example.

The trepanematoses: syphilis, yaws and pinta

The group of diseases known as the **treponematoses** are chronic or subacute infections caused by micro-organisms called spirochetes of the species *Treponema pallidum*. The infection is divided into 4 types: pinta, yaws, endemic (non-venereal) syphilis and venereal syphilis. Pinta is geographically confined, being found only in tropical regions of America (Mexico to Ecuador). Yaws affects populations with a low level of hygiene in tropical and subtropical humid areas. Endemic syphilis is present in rural populations in temperate and subtropical non-humid areas. Venereal syphilis is the most widespread form occurring in urbanized populations in all geographic regions. It is caused by *T. pallidum pallidum*. DNA sequence homology suggests that all the treponemes are very closely related and human cross-immunity exists between the syndromes. There are several theories concerning the origins and spread of syphilis. It is clear that: 1) syphilis existed in pre-Columbian America; 2) syphilis was present in Europe prior to the 1495 epidemic. Yet both Europe and the Americas experienced epidemics of syphilis after first contact. The explanation for this may be that both the New and Old World human populations carried their own specific variant, which proved virulent to the other. Certainly there appears to have been some resistance among New World populations to their own variant. Concerning syphilis in prehistory, it is likely that only saprophytic infections or infections of a low grade of pathogenicity could have survived. With population increases at the origin of agriculture, strains of pathogens producing more acute infections could exist. Rapid transit of pathogens through multiple hosts, as encouraged by sexual practices in Europe during the 15th century, tends to increase the virulence of pathogens.

Mycobacterial diseases: Tuberculosis and Leprosy

Tuberculosis in humans is an acute or chronic infection of soft or skeletal tissues by *Mycobacterium tuberculosis* or *M. bovis*. Most bacteria of this genus are free living saprophytes (grow on decomposing material). Tuberculosis is a world-wide disease that can flourish in almost any climate. Reservoirs of infection with *M. tuberculosis* are usually other humans infected with the pulmonary form of the disease. Transmission of *M. tuberculosis* from animals to humans is rare, but does occur. Most animal infections are due to *M. bovis*. Host factors appear to play a major role in determining the likelihood of infection. Poor nutrition, poor socioeconomic status with overcrowding, a compromised immune system and age are all important. This means that abrupt, severe demographic changes that accompany war or social disruption are often associated with equally abrupt and marked rises in the incidence of tuberculosis. Most identification of tuberculosis in ancient human remains depends on skeletal changes associated with the disease (e.g. vertebral destruction – Pott's disease of the spine). Evidence of tuberculosis in bony tissue first appears in the neolithic of Europe (Arene Candide cave in Italy – dated by the radiocarbon method at 5,500 to 6,000 ya). It is uncertain whether tuberculosis was present in Asia at the same time. Native American remains showing signs of tuberculosis have been found which date to pre-Columbian times, suggesting the existence of some form of tuberculosis, probably contracted from buffalo. In addition, *M. tuberculosis* DNA has been sequenced from a Nazca mummy dated at 1,300 ya, indicating quite clearly that *M. tuberculosis*, and hence pulmonary tuberculosis, was probably of worldwide extent prior to European colonization of the new world. The epidemics of tuberculosis which ravaged native Americans during the 17th, 18th and 19th centuries were probably due more to social disruption, forced aggregation and poor living conditions rather than the *de novo* exposure of an immunologically naïve population to a newly introduced disease from the Old World.

Leprosy (**Hansen's disease**) probably originated in East Africa or near East by transfer of a naturally occurring mycobacterium into the human population. It travelled by trade routes throughout the Old World during the Iron Age. It affects periphery of body, causing scarring and nerve damage that eventually leads to loss of parts of the face and the digits.

How do new diseases enter the human population?

Clearly several factors can be responsible for the emergence or acquisition of new infectious diseases:

- Transfer of novel pathogens from either domesticated animals or wild animals (e.g. HIV, *Mycobacterium bovis*)
- Changes in farming practices bringing humans into contact with potential pathogens (e.g. slash and burn agriculture and malaria)
- Changes in population density providing readier spread of pathogens (e.g. mumps and measles)
- Changes in cultural practices influencing transmission (e.g. syphilis)
- Contact with infected foreigners (e.g. smallpox)

Human culture and HIV/AIDS

HIV is a good example of an infectious disease newly introduced to the human population, whose path of entry and manifestation is greatly influenced by human cultural practices. The type of HIV responsible for the AIDS epidemic is HIV-1. A far less common type is HIV-2 which is found only in West Africa and is less virulent and more genetically diverse than HIV-1. HIV-2 is believed to have evolved from simian immunodeficiency virus (SIV) present in African monkeys (sooty mangabeys) and is almost genetically identical to that virus. Recent studies also indicate that HIV-1 is derived from a variant of SIV infecting chimpanzees (*Pan troglodytes*). The virus crossed into humans to become HIV-1 some time during the early to mid-twentieth century. Transfer to humans probably occurred due to the hunting and butchering of chimpanzees for bush meat. Throughout sub-Saharan Africa, AIDS is of course now an epidemic, much more serious than its manifestation in the west. In some sub-Saharan countries the incidence of HIV/AIDS appears to be linked to other sexually transmitted infections like chancroid and infection rates of both chancroid and sexually transmitted HIV can be positively influenced by human cultural practices like male circumcision.

Adaptation of HIV to the human population

HIV is a good recent example of the adaptation of a pathogen to its host. HIV is the most mutable and genetically variable virus known. The strain of HIV which causes human AIDS is HIV-1, which seems to have a similar DNA sequence to the strain of SIV (simian immunodeficiency virus) which infects chimpanzees. Chimpanzees are commonly hunted and eaten in those parts of West Africa where AIDS arose, so it appears likely that human HIV-1 is derived from chimpanzee SIV and crossed the species barrier as a result of the hunting and butchering of chimpanzees. SIV has minimal effects on chimpanzees, probably because the host and pathogen have co-adapted over several hundred thousand years. Once SIV entered the human population (some time in the 1950s or perhaps earlier?), mutating to HIV, it immediately began to cause serious illness. The virulence of HIV will doubtless decline in the future as less virulent strains are selected for.

HIV is being brought under control in Western nations but continues to be a major health problem in developing countries.

Lecture 22 Malaria and human evolution

Specific Objectives

1. To define the terms gene pool, genetic load and heterozygous advantage in terms of the relationship between malaria and human populations.
2. To be able to describe the relationship between the malaria parasite life cycle and a number of red blood cell disorders.
3. To describe the global distribution and impact of malaria and its influence on the genetic diversity of human populations.
4. To be able to discuss the origins and spread of the malaria and human parasite-host relationship.

Micro-organisms and parasites place considerable selection pressure on humans. A good example is **malaria**. This is an illness that is constantly present (**endemic**) in many areas of the world. Its history and biology have made a considerable impact on human diversity and health.

Genetics of populations

Every population of a species carries the same allele variations of their genes on the chromosomes of its individuals. The proportion of each allele in different populations usually occurs with stable frequencies. These frequencies are subject to **selection pressure**. This genetic diversity within a population is known as its **gene pool**. An allele that confers a disadvantage to the individual is called a **deleterious allele** and should occur with low frequency. These are usually recessive traits that are compensated by the normal allele in the heterozygote (normal phenotype) but severely reduce fitness, or are lethal, in the recessive homozygote. Such alleles stay hidden in the population till the occasional affected individual is born. The number and frequencies of deleterious alleles in the gene pool is the **genetic load** of the population. These are also a source of hidden variation on which changing selection pressures can act.

Distribution of anaemia and malaria

Deleterious alleles include those that cause inherited blood disorders. These have defective red blood cells and produce clinical anaemia. The geographic distribution of high frequencies of anaemias coincides with the geographic distribution of malaria, a parasitic infection of red blood cells. This was first noticed for the occurrence of the sickle cell anaemia in West and Central Africa, and regions around the Mediterranean, Middle East and India.

If an individual inherits the sickle cell allele (Hb^s) from both parents, then life expectancy can be very short (childhood), even with aggressive medical treatment (less than 45 years). The red blood cells change shape in low oxygen stress (sickle) and do not function properly. These individuals are resistant to malaria but the blood disease is debilitating and potentially fatal. It should occur with a low frequency.

It also turns out heterozygous individuals, who carry one normal and one sickle cell allele in each of their cells, are resistant to malaria. Only the infected red cells will change shape (sickle) and these are recognized by the immune system as abnormal and are destroyed. Hence, heterozygous individuals get very mild or sub-clinical illness. On the other hand, the homozygous “normals”, without any copies of the defective allele, get full blown malaria. The heterozygous carriers are actually protected from malaria. This association is called **heterozygous advantage**, where malaria is the selective force. Having one copy of a deleterious allele confers increased fitness. Natural selection ensures that the frequency of this allele is kept at a higher level in the gene pool than would normally be expected. This is also true for other inherited anaemias.

What is malaria?

Malaria is a parasitic infection of blood. It is characterised by fever, chills, and anaemia. The parasite is a single celled organism (protozoan) of the genus *Plasmodium*. There are several species (*P. falciparum, P. vivax, P. malariae, P. ovale*) that vary geographically and cause malaria of different severities. The parasite vector (carrier) is a mosquito of the genus *Anopheles*. There are different species (*A. gambiae*, *A. funestus*) that do better in the wet or dry seasons respectively.

The parasite is injected into the bloodstream in mosquito saliva when an infected mosquito bites to feed on blood. The saliva contains anticoagulants to keep the mosquito's meal liquid. The *Plasmodium* parasites first infect and multiply in liver cells, which they destroy before moving to red blood cells that pass through the liver. Each time they rupture red blood cells they cause a bout of fever, chills, anaemia and other complications. Some of the multiplying parasites in the red cells form gametes (sex cells) which await ingestion by the next mosquito to bite. Inside the mosquito gut the *Plasmodium* gametes undergo sexual union and the newly formed next generation of parasites moves to the salivary glands to be injected into another host with the next bite.

Origin and spread of malaria

It is thought that before the development of agriculture, humans rarely if ever lived close to mosquito breeding areas. With the development and spread to Africa of slash-and-burn agriculture (2,000 to 3,000 years ago) penetration and clearing of tropical rain forests occurred for the first time. As a result of deforestation, mosquitoes had to leave the missing canopy and move to open stagnant pools on the ground. They also had to find new hosts to feed on. Human agricultural settlements around the cleared land would have provided prime mosquito breeding areas in close proximity to a new food source for both the mosquito and its parasites.

Mosquitoes need sugar meals for energy and feed on nectar. The female mosquito also needs protein meals to develop her eggs. Only the female feeds on blood. Mosquitoes also need still water for egg laying, the larval and pupal stages of their life cycle, and to emerge and settle on as adults before they can fly. Any stagnant water that lasts for at least 2 weeks (dependant on temperature) is all it needs to maintain mosquito populations. Disturbed ground from land clearing and farming, as well as discarded broken containers, would have provided a continuous habitat in close association with humans.

Malaria became endemic in the Old World, from Africa to around the Mediterranean, Middle East and Asia, with concomitant selection pressure for disease resistance. Both the mosquitoes and the parasites were introduced to the New World with European exploration and settlement in the 17th century. This was amplified and maintained by the slave trade that brought new waves of mosquitoes and infection on slave ships, in combination with massive land clearing for agriculture and cramped nearby housing for slaves. Slave dependent agriculture and malaria spread across southern North America, the Caribbean islands, Central America, and eastern South America. In West Africa, black coastal tribes made inland invasions to capture and collect slaves for sale to the white slave traders. This spread malaria across inland Africa.

Currently, malaria occurs across much of Africa, western Mediterranean regions, the Middle East, India, South East Asia and across Indonesia to New Guinea. It is also endemic in Central and South America.

Along with slaves, mosquitoes and malaria, adaptive resistance strategies in the form of various anaemias were also exported. This occurred with black African slaves and white indentured European workers, who added their inherited diseases to the New World mix.

Deleterious alleles and anaemia

The haemoglobin of red blood cells is made of four protein chains. All adults have Haemoglobin A (HbA) comprising two α chains and two β chains that bind oxygen loosely and give it up to tissues easily. This differs from the foetus, which has Haemoglobin F comprising two α chains and two **γ** chains that bind oxygen tightly and give it up to tissues reluctantly. Genetic coding errors (mutations) that alter this can give rise to defective red blood cells and produce a variety of anaemias. Deletion errors that lead to insufficient α chains produce α thalassaemia, which relies on extra β or **γ** chains that leave tissues oxygen starved. Errors in coding control genes lead to insufficient or absent β chains that produce β Thalassaemia, which relies on α chains only (unstable) or continuation of HbF leaving tissues oxygen starved. Further, a variety of substitution errors in the β chain genetic code changes one amino acid and causes folding errors in the molecule. These produce sickle cell anaemia (Haemoglobin S), as well as Haemoglobin C, Haemoglobin D and Haemoglobin E anaemias. All of these anaemias vary from very severe in the homozygous recessive form to very mild in the heterozygotes. Double heterozygotes for one allele of each of any two of these anaemias usually produce severe disease.

An inherited X-linked enzyme deficiency anemia is also common. The enzyme glucose-6-phosphate dehydrogenase is necessary for conversion of glucose to energy available for red cell use. Deficiency of this enzyme (G6PD deficiency) makes red cells very susceptible to oxidative stress, which can be brought on by low environmental oxygen, drugs (including anti-malarial drugs), infections and certain foods (e.g. fava beans). The action of these triggers can multiply the anaemia response so severely that it can be lethal. In fact, G6PD deficiency was first properly studied and understood in the 1950's when African American and Italian American soldiers were studied after it was found that some of them were dying from the anti-malarial drug primaquine given to all soldiers sent to Korea. Similarly, oxidative foods such as fava beans confer malaria protection to the normal population but can make men with G6PD deficiency quite ill.

Malaria and genetic diversity of human populations

Haemoglobin in red blood cells is the protein food for both the mosquitoes and *Plasmodium*. However, the parasite must live in intact red cells while reproducing (sexually and asexually). Any change to red cells that affects the integrity of their structure and function will have adverse effects on both the human host and the parasite. As malaria began to have an impact on human populations, selection pressure favoured the retention and spread of inherited anaemias as a biological adaptation for disease resistance. Across the Old World these genetic traits became regional in areas with endemic malaria. Sickle cell anaemia occurs mostly in Western and Central Africa but also across the Mediterranean and in pockets of the Middle East and India. β Thalassaemia is prevalent across Mediterranean Europe and the Middle East whereas α thalassaemia occurs across the malarial areas of the Far East. Haemoglobin C is in West Africa, Haemoglobin D is in western India, and Haemoglobin E occurs across South East Asia and

Indonesia. G6PD deficiency variants cover the entire range of malaria distribution. Many individuals carrying these diseases can also be found in the malarial areas of the New World and across North America, where there is no malaria.

Malaria and anaemia – past and present

Malaria is still a problem in many places around the world. In those countries with poor access to modern medicine, malaria continues to provide a potent selection pressure for blood disorders (anaemias) where heterozygous advantage continues to maintain high deleterious allele frequencies. However, in those countries with no malaria but good access to modern medicine, especially North America, high deleterious allele frequencies are is still maintained. With intensive medical intervention many homozygous recessive individuals not only survive, they live longer with relatively good health, so there is no selection pressure beyond genetic counselling to reduce the genetic load of the population. It still remains a serious health issue to the families of those suffering from anaemia or carrying an anaemia allele.

It is also important to note that humans are not the only species subject to selection pressures in this relationship. Selection pressure is also ongoing on the malaria parasites to develop resistance to new drugs and new immune responses by the host. Similarly, selection pressure continues on the parasite vector in the form of habitat change and insecticides from mosquito eradication programs.

Note that both the mosquitoes and *Plasmodium* parasites have short generation times and they both reproduce sexually, with the generation of diversity that meiosis produces. This makes these species very responsive to selection pressures and rapid evolutionary change and, consequently, very hard to eliminate.

Medicine Teaching Laboratory Student Risk Assessment		Gross Anatomy Practical Classes for Medical and Science Students DOC:PHSL-SRA-S&H-01rev1.1

Hazards	Risks	Controls
Physical Cold temperature (16°C) Sharp bone/plastic Biological Fungi, bacteria (tetanus), hepatitis B and C Chemical Formaldehyde Methanol 2-phenoxyethanol	 Cold Penetrating wound of foot Infection Corrosive/Flammable Irritant/toxic Irritant	• Wear laboratory coat over appropriate warm clothing • Wear enclosed shoes with full coverage of the dorsum of the foot • Have appropriate immunisation • Do not eat, drink or smoke in the Gross Anatomy Lab • Do not place anything (e.g. pens, pencils) into your mouth • Use disposable gloves when handling wet specimens and do not cross-contaminate models or bones with wet specimens • Always wash hands with liquid soap and dry thoroughly with disposable paper towel before leaving • Low concentrations of chemicals used • Chemicals used in well ventilated area • Safety Data Sheets for chemicals available in the laboratory

Personal Protective Equipment required

Emergency Procedures

In the event of an alarm sounding, stop the practical class and wait for confirmation to evacuate from demonstrators. Then wash your hands and pack up your bags.
Follow the instructions of the demonstrators regarding exits and assembly points.

Clean up and waste disposal

- Cover wet specimens with the towels provided. Make sure that towels do not hang over the edge of the table, because this allows fluid to drip onto the floor. Fluids on the floor are a major safety hazard and should be reported to staff immediately.
- Replace stools under the tables in your cubicle.
- Remove your gloves and dispose in the biowaste bins provided.
- Wash your hands and instruments thoroughly with the soap provided and dry your hands with the paper towel.
- Remove your laboratory coat when you leave the dissecting room.

Ethics Approval

This type of practical has been previously considered and approved by the UNSW Human Research Ethics Advisory Panel (HREC09372).

Declaration

I have read and understand the safety requirements for this practical class and I will observe these requirements.

Signature:……………………………………………………………Date:……………………………

Student number: ………………………………………………………

ANAT-SRA-Med&SciStudent relates to RA-MED-06. Date for review: 1/2/2017

Practical 1 Primate musculoskeletal anatomy

Specific Objectives:

1. To know and identify the major bones of the axial skeleton, upper and lower limb (see learning activities).
2. To be able to identify major components of primate cranial anatomy including the orbit, frontal, parietal, temporal, sphenoid and occipital bones, mandible, temporomandibular joint, foramen magnum, and features of the masticatory (chewing) apparatus.
3. To be able to indicate the major anatomical, functional and behavioural differences between primates and other mammals.
4. To review major groups of living primates, noting their characteristic features and relationships.

THE RELEVANCE OF ANATOMICAL DETAIL AND THE USE OF SPECIMENS

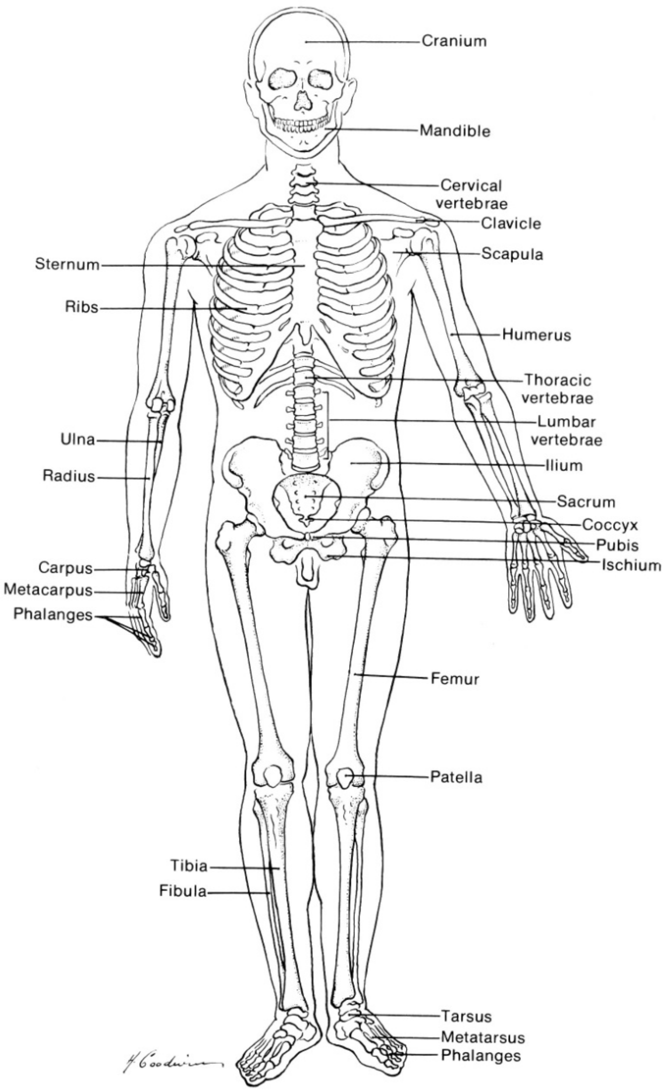
It is necessary to gain familiarity with basic structures, such as bones, teeth, muscles and brain. They will regularly be compared between primates, early hominins and modern humans. Some medical terminology will be used because these words are the language of the scientist and are used in museums, books, documentaries, CDs, websites and publications. They will make more sense as you hear them used in context during lectures and practical classes.

To appreciate why we make these cross-species comparisons it should be emphasized that humans have evolved from a quadruped primate ancestor to a bipedal species. We will look at bipedal specializations in detail in order to understand the changes and compromises that have been made from the basic inherited quadrupedal architecture.

Learning Activities:

This practical class has three general aims. The first is to familiarize you with the major bones of the skeleton so that you will be better equipped to understand our subsequent discussion of hominin structure. The second is to emphasize the differences between primates and other mammals. The third is to develop an awareness of the different types of living primates.

1. The skeleton of all mammals is divided into two groups of bones, which are readily identified on an articulated human skeleton. These are the axial and appendicular parts of the skeleton. The **axial skeleton** consists of the **skull**, **vertebral column** (including the **sacrum**), **hyoid bone**, **ribs** and **sternum**. The vertebral column is divided into **cervical**, **thoracic**, **lumbar**, **sacral** and **coccygeal** segments. Examine typical vertebrae from each part of the vertebral column. Note the curvature of the different parts of the vertebral column (concave anterior - **kyphotic** - in thoracic and sacral regions, concave posterior – **lordotic** - in cervical and lumbar regions). The hyoid bone is a small bone in the neck and will be important for us when we discuss speech, because it provides attachment for some of the tongue muscles. The **appendicular skeleton** is that part of the skeleton associated with the upper and lower limbs. The upper limb bones are joined to the axial skeleton by the **pectoral girdle** (consisting of **scapula** and **clavicle**) and the lower limb by the **pelvic girdle** (consisting of the large **hip bones** or ossa coxae, which actually represent the fusion of three parts called the **ilium**, **ischium** and **pubis**). Identify the **radius**, **ulna** and **humerus** in the upper limb and the **femur**, **tibia** and **fibula** in the lower limb. The hand is known in biology as the **manus**, whereas the foot is called the **pes**. Bones of the wrist are collectively called the **carpals**. Bones of the proximal part of the foot are collectively called the **tarsals**.



View a demonstration of the movements of **pronation** and **supination** by your tutor. Pronation involves rotation of the radius around the ulna so that the palm of the manus faces downwards, whereas supination is rotation in the opposite direction (i.e. palm ends facing upwards). Visit the Anatomy Museum and try to find these bones in the skeletons of other primates.

2. The skull is particularly important for us in this course. Broadly speaking, the hominin skull consists of a bony face and a cranial cavity, which encloses and protects the brain. Identify the bony plates that form the vault of the skull (**frontal**, **parietal** and **occipital**). On the side of the skull lies the **temporal** bone, with a prominent **mastoid process** in modern humans. A key opening in the temporal bone is the **external acoustic meatus** for transmission of sound to the middle ear. Identify the **coronal suture** between frontal and parietal bones, the **sagittal suture** running down the midline and the **lambdoid suture** between parietal and occipital bones. The base of the skull is formed by the **occipital** bone and a centrally-placed **sphenoid** bone. Note the presence of **occipital condyles** on the underside of the skull for articulation with the first cervical vertebra (the **atlas**). The occipital bone has an opening called the **foramen magnum**, through which the spinal cord emerges and two of the arteries to the brain (the vertebral arteries) will enter the skull. The **hypoglossal canal** also allows the hypoglossal nerve to the tongue muscles to exit

the endocranial cavity immediately above the foramen magnum. The skull base has multiple openings for transmission of nerves and vessels. Identify the **carotid canal** (transmitting the internal carotid artery) and the **jugular foramen** (transmitting the internal jugular vein and some cranial nerves: glossopharyngeal, vagus and accessory). The bony face has the central **piriform** (meaning pear-shaped) **aperture** for the nasal cavity and the two forward facing **orbital cavities**. The **maxillary bone** (**maxilla**) makes up the bulk of the modern human cheek. Identify the **mandible** and the two arcades of teeth in the upper and lower jaws. The teeth are set in the **alveolar margins** of the **maxilla** and **mandible**. Note that the mandible articulates with the skull by paired **temporomandibular joints**.

3. Primates are often considered to share several anatomical and behavioural characteristics, which set them apart from other mammals. Try to identify these features on skeletons in the museum and on your colleagues! These characteristics include:

a) a tendency towards upright posture, associated with sitting, leaping or standing. Hominins take this a step further to upright walking.
b) a behaviourally flexible and generalized limb structure. Primates have retained some bones (e.g. the **clavicle**) and some abilities (e.g. rotation of the forearm) that have been lost in other mammals. Discuss the functional significance of the **clavicle**.
c) hands and feet with a high degree of **prehensility** (grasping ability). This is associated with:
  - retention of five digits on the hand.
  - opposable or partially opposable thumb (not seen well in all primates).
  - nails present instead of claws.
  - sensitive pads at the ends of digits.
  - ability to rotate the radius of the forearm (along with wrist and hand) around the ulna (**pronation**/**supination**).
d) generalized dentition indicating a relatively unspecialized diet.
e) well developed visual system function with stereoscopic vision (i.e. depth perception as facilitated by forward facing eyes) and often with colour vision (not in nocturnal primates).
f) expanded brain (increased encephalization).
g) decreased reliance on the sense of smell (olfaction).
h) social/lifestyle features such as prolonged lifespan, longer periods of gestation, greater dependence on flexible, learned behaviour, and a tendency to live in social groups and follow diurnal patterns of behaviour (daytime activity).

4. The primate skull shows several distinctive features. On human, modern ape and *Dryopithecus* (fossil ape) skulls note the generalized dentition with a typical old world primate <u>dental formula</u> of two **incisors**, one **canine**, two **premolars** and three **molars** on each side of each dental arch. Identify the **roots** and **pulp cavity** of each type of tooth. How many roots do molars usually have? What is the role of the roots and pulp cavity? Discuss the difference between **primary** or **deciduous (milk) teeth** and secondary or permanent teeth with your tutor. View examples of primary deciduous teeth (2 incisors, 1 canine, 2 molars in each quadrant) on the skulls of juvenile humans. Which is the last permanent tooth to erupt and when does this happen? Contrast primate teeth with the dentition of a carnivore (e.g. a dog or a seal) or a herbivore (e.g. a wallaby). Discuss the roles of these different types of teeth with colleagues and your tutor. Incisors are specialized for slicing food, canines for gripping food, premolars and molars for grinding/crushing food. Note that

the **lower first premolar** is semisectorial in many primates (i.e. up to and including some australopithecines). This means that the tooth has a sharp edge that engages with the canine to assist in tearing/cutting of food. Note the forward facing orbits and the presence of a **post-orbital bar or plate** in the haplorhine primates. Examine the shape and orientation of the orbit in the dog or wallaby skull and contrast with that in a typical primate skull from the museum. In hominins and apes the post-orbital plate is called the lateral wall of the orbit.

Practical 2 Cranial anatomy of australopithecines and early humans

Specific Objectives:

1. To identify the main anatomical features of the skulls of robust and gracile australopithecines, *Homo habilis*, *Homo erectus* and *Homo sapiens* and relate these features to function.
2. To identify the major differences in cranial anatomy between early members of genus *Homo* (e.g. *Homo habilis)* and australopithecines, with a consideration of the functional relevance of the changes.
3. To summarize the major anatomical changes in the transition from earliest members of genus *Homo* to *Homo erectus*.
4. To indicate the type of climate during which *Homo erectus* emerged from Africa and diversified.
5. To be able to discuss the diversity of *Homo erectus* types throughout the Old World and indicate the significance of the wide dispersal of this hominin.
6. To be able to summarize the main anatomical features of archaic types of *Homo sapiens* including Neandertals.

Learning Activities:

1. Study the cranial models of robust (*A. boisei* and *robustus*) and gracile (*A. afarensis* and *africanus*) australopithecines. Note that originally the term robust was intended to indicate differences in body mass between the two groups, but this is no longer thought to be true. Nevertheless, there are significant differences between robust and gracile australopithecines in cranial anatomy (face and dentition) that also fit the adjectives. Gracile australopithecines have more lightly built faces with small **temporal and infratemporal fossae**, while robust australopithecines have a prominent **sagittal crest, postorbital constriction of the skull, broad faces, thick zygomatic processes** and **large temporal and infratemporal fossae**. Note also the broad vertical face of the robust types. What is the functional significance of the crest, postorbital constriction and broad face in these robust hominins?

2. Nevertheless, the most significant difference between the robust and gracile forms lies in the teeth. Note that the robust forms have relatively large teeth, with deep jaws and greatly enlarged back teeth, particularly molars. What does this tell us about the lives of these creatures? Note also that gracile forms have proportionately larger front teeth compared to back teeth. This difference between robust and gracile forms is most clearly seen in the relative size of the **canine** and **first premolar**. In robust forms the first premolar is twice as large as the canine, while in gracile forms the first premolar is only about 20% bigger than the canine. Discuss the reasons for this with your colleagues and tutor.

3. Look at the shape of the jaw in the australopithecines and compare this with both the modern ape and modern humans. What do you notice about the shape of the **alveolar arch** that supports the teeth? Which apes and hominins have a “U” shaped jaw and which have a semicircular jaw? Are there intermediate forms?

4. In popular culture we still hear reference to the search for the “missing link”. Why is this idea not particularly useful in thinking about human evolution? What are the hidden assumptions behind the term?

5. Study the skull model of *Homo habilis*. What do you notice that differs from the australopithecines? Louis Leakey, who discovered the early *H. habilis* remains, pointed out the presence of larger front teeth relative to back teeth and narrower premolars in the early *Homo*, but what is the most significant difference?

6. Share around the three different fossil models of *Homo erectus* and compare them with the modern human skull and *H. habilis*. Look for some of the characteristic skull features of *H. erectus* like the **nuchal torus**, a ridge of bone at the back of the skull, and prominent **supraorbital ridges**. Note that the vault of the skull is long and low, receding back from the brow ridges with little forehead development. Interestingly, the cranium is wider at the base than both earlier *Homo* and later *H. sapiens.* With *H. erectus* the maximum breadth of the skull is below the ear opening (giving a pentagonal profile), while both earlier and later *Homo* have more vertically sided skulls with the maximum breadth above the external ear opening. Compare the shape of the skulls as viewed from behind: *H. erectus* has a pentagonal shape, while modern *Homo* is more circular or globular. What do you notice about the shape of the **alveolar arch** compared to australopithecines? Note that some *H. erectus* specimens (the earliest examples) show "**shovel-shaped incisors**". This tooth shape may resist wear and is also seen in Neandertals. It is occasionally seen in modern humans (e.g. some modern Asians and native Americans).

7. With colleagues and your tutor discuss the evidence concerning the way of life of *H. erectus* in Africa, Java and China. What was the world's climate like at the time at which *H. erectus* lived? How would *H. erectus* have coped with the harsh environment of northern China at that time? What did the excavations at Zhoukoudian tell us about these peoples?

8. Study the examples of early archaic *H. sapiens* (Kabwe/Broken Hill) and late archaic *H. sapiens* (Neandertal). The Kabwe specimen shows massive browridges, low cranial vault and a prominent occipital or **nuchal torus**, but has a cranial capacity within the range of modern *H. sapiens*. Late archaic *H. sapiens* like the Neandertals showed large arching browridges (**supraorbital ridges**) with a low forehead, projecting midface, lack of chin, an **occipital bun** (a posterior protuberance of the occipital bone associated with robust postvertebral muscle attachments), but a large cranial capacity (average around 1600 ml, even bigger than in modern humans).

9. Now look at the examples of modern *H. sapiens* (Cro-Magnon, Kennewick, modern African, Pueblan, Australian) noting the **vertical forehead** and **relatively small browridges**, **canine fossa** below the orbit, **pyramidal mastoid process** behind the ear, **prominent chin** and **small anterior teeth**. What change in facial anatomy gave rise to the canine fossa and prominent chin? What might this tell us about how the lives of anatomically modern humans differed from those of archaic forms?

10. <u>Discussion of Films</u>: *Portrayals of human ancestors*

Ideas about how human ancestors looked and behaved are often influenced by events and ideas in our own society. What is more, those ideas about human ancestors can often influence popular culture. In other words there is an ongoing interaction between the modern world and perceptions about human evolution. The two films shown illustrate examples of this interaction.

When you watched the two films (the opening scenes of *2001: A Space Odyssey* and the portrayal of australopithecines in *Walking with Beasts*) did you ask yourself the following questions:

- What ideas about early hominin behaviour are being portrayed in the film? What is being said about co-operation, aggression, social structure, tool use and upright walking?
- What has influenced the way that the hominins' behaviour is presented? Is it popular culture, the whim of the director/animator, reasoning by analogy from apes or fossil evidence?
- Is there an attempt to convey a message of significance for the modern world? Is that message valid?

11. *Assessing cultural development among humans*

It is often assumed that human communities have developed according to a set pattern in different geographical locations over time. This pattern is always described as a shift towards more complex societies in terms of a series of changes, where a nomadic lifestyle is replaced by a sedentary lifestyle. The reason for this change is interpreted as a shift from a subsistence economy based on hunting and gathering, to a settled or urban one based on the production of excess resources. Initial settlement in one place is attributed to the development of agriculture with the domestication of plants and animals. Over time, specialisation and the development of industries, such as pottery and tool manufacture, increases. These changes are associated with technological developments, like the use of metal to replace stone tools. This process is thought to culminate in the establishment of urban centres.

Practical 3 The human lower limb and bipedal locomotion

Specific Objectives:

1. To identify the main bones of the lower limb (see learning activities).
2. To identify the main skeletal and ligamentous features associated with bipedal locomotion in hominins and discuss the functional significance of each.
3. To be able to list and discuss recent ideas concerning the reasons for the emergence of bipedalism in hominins.

Learning Activities:

1. Use modern human bones and specimens to identify the anatomical features associated with bipedal locomotion. Study the lower aspect of the human skull, noting the position of the **foramen magnum** (through which the spinal cord connects with the brain) and the joint between the skull (**occipital condyles**) and the first vertebra (**atlas**) of the neck (**atlanto-occipital joint**). Measure the distances from this joint to the front and back of the skull, respectively. What is the functional significance of the central position of this joint in modern humans? Now examine the model of an ape skull and identify foramen magnum and atlanto-occipital joint, and make the same measurements. What do you notice about the position of the foramen magnum and atlanto-occipital joint in the ape skull? Make the same measurements in the skulls of representative hominins. Study the area of the skull posterior to the occipital condyles in the various models and skulls. Which specimens have the roughest occipital bones, indicating attachment sites for strong post-vertebral muscles?

Species	Distance from front of skull to atlanto-occipital joint (A) (in cm).	Distance from back of skull to atlanto-occipital joint (B) (in cm).	Ratio of A/B expressed as *x*:1
Gorilla (*Gorilla gorilla*)			
Chimpanzee (*Pan troglodytes*)			
Robust australopithecine (*A. boisei*)			
Gracile australopithecine (*A. africanus*)			
H. habilis			
H. erectus			
H. sapiens			

2. Study the **vertebral column** of an articulated human skeleton. What do you notice about the variation in the size of the **vertebral bodies** as one proceeds down

the vertebral column? What is the functional significance of this? Now look at the vertebral column of a primate skeleton in the museum. Is the change in vertebral body thickness and width as prominent as in the human? Note the **curvatures** of the modern human vertebral column. Where are these located and what is their significance? Are they present throughout life? Are they noticeable in the vertebral column of a non-human primate? When do these curvatures appear during development?

3. Compare the hip-bone of the human with that of an ape and an australopithecine. Identify some key anatomical features on the hip bone and sacrum (**iliac crest**, **gluteal and pelvic surface of ilium**, **pubic body**, **superior pubic ramus**, **ischiopubic ramus**, **ischial tuberosity and spine**, **sacral promontory**) of apes, australopithecine and modern humans. Note the short, broad **iliac blades** in the human and australopithecine (*Australopithecus afarensis* – Lucy). The gluteal surfaces of the hip bones of the ape face posteriorly, whereas those of the human and australopithecine face more laterally. The human **pelvis** is basin shaped (in fact, *pelvis* is Latin for basin), whereas the ape pelvis is more elongated with iliac blades lying alongside the lower vertebral column. What is the significance of this for weight-bearing function? Rotational forces at the sacroiliac joint are resisted by the **sacrotuberous** and **sacrospinous ligaments** in modern humans. The sacrospinous ligament was originally a muscle (ischiococcygeus in prehominins and hominins), but this muscle has been partially converted to a ligament (sacrospinous ligament) in the upright walking hominins.

Note that the external **gluteal surface** of the human hip-bone faces laterally and houses the **gluteus medius** and **gluteus minimus** muscles. These muscles attach to the femur and are important (particularly the gluteus medius) for supporting the weight-bearing hip during the stance phase of the human bipedal stride. Note also the large **gluteus maximus** muscle in humans. This muscle arises from the gluteal surface and attaches to the back of the femur. It is an important and powerful muscle in extending (straightening) the thigh during climbing and running.

4. Using the articulated human skeleton, measure the lengths of the femur, tibia, humerus and radius. Compare the relative lengths of these bones with those in a non-human primate skeleton from the anatomy museum. What do you notice about the relative lengths of upper and lower limb bones? What is the functional significance of this? Look closely at the human femur and the angle between its long axis and the plane of the **tibial plateau**. The **femur** is angled inward to bring the knee joint beneath the centre of gravity of the trunk. What is the functional significance of this arrangement? The lower end of the femur has large ellipsoidal **femoral condyles**. During extension of the knee the arrangement of ligaments (**anterior cruciate**) and condylar shape permits locking of the knee in extension, thereby making long periods of standing more economical. The upper surface of the tibia has a relatively flat surface (**tibial plateau**) that is deepened by the presence of the medial and lateral menisci. What is the role of the menisci? Study illustrations of the femur of *Australopithecus afarensis* ("Lucy") and an ape, looking for the presence of the features already noted in the modern human femur. What do you notice?

5. Study the bones of the modern human foot (**pes**), identifying the **tarsals** (in particular **medial cuneiform**, **talus** and **calcaneus**), **metatarsals** and **phalanges**. Note the medial cuneiform shape in humans and compare this with the gorilla. What do you notice? Note the arrangement of foot bones to form an arch (**plantar arch**). Study the dissected foot specimen to identify the ligaments (**spring** and **plantar**

ligaments) and tendons of muscles associated with support of the plantar arch. Note the orientation of the phalanges of the great toe, in line with the other toes. Discuss the contribution of plantar arch support and the parallel configuration of toes to bipedal walking. Why is the "big toe" (digit 1) so important for walking? Look at the model of the Laetoli footprints (juvenile and adult). How do they compare with a modern footprint?

6. Discuss with colleagues and your tutor the possible reasons and mechanisms for the emergence of bipedalism in hominins. Which models are supported by paleoanthropological evidence? Are the different models mutually exclusive?

Factor	***Speculated influence***	***Comments***
Carrying of objects (tools, infants, weapons)	Upright posture freed the hands to carry various objects.	
Hunting	Carrying weapons and energy saving long distance walking made hunting more efficient.	
Seed and nut gathering	Feeding on seeds and nuts is easier while standing upright.	
Feeding from bushes	Upright posture provided greater reach to lower branches to access seeds, nuts, berries, fruit, etc.	
Visual surveillance	Standing up allowed a better view to sight predators or other group members.	
Long distance walking	Energy efficient bipedal walking made long distance foraging easier, even though it is more energy costly than quadrupedal running.	
Male provisioning *(suggested by Lovejoy)*	Males obtained and carried back resources (e.g. food) to females with dependent offspring.	

Practical 4 Human childbirth

Specific Objectives:

1. To identify, on models and specimens, the uterine body, tubes and cervix, ovary and vagina, noting the close relationship of the female reproductive tract to the urinary bladder, rectum and anus.
2. To indicate the major axes of the birth canal on models and specimens.
3. To identify features on the female pelvic model which influence the size of the birth canal (ischial spines, sacral promontory, subpubic angle) or contribute to turning of the fetal head (sacrotuberous and sacrospinous ligaments).
4. To identify the major features of the fetal skull (frontal, parietal and occipital bones; anterior and posterior fontanelles), indicating the major obstetrically significant skull dimension (suboccipitobregmatic).
5. To be able to describe the stages in movement of the fetal head through the birth canal, indicating rotational movements at each level.
6. To be able to indicate the obstetrical, behavioural and cultural significance of the occipitoanterior position of the human fetal head during emergence of the infant.
7. To consider the biological and cultural significance of prolonged postnatal brain growth in human infants.

Learning Activities:

1. Using models and specimens of the human female pelvis identify the major components of the female reproductive system (**uterine body**, **uterine tubes**, **uterine cervix with intravaginal and supravaginal parts**, **ovary** and **vagina**). Note that the vagina and uterine cervix are closely related to the **rectum** and **anus** behind, while the **urinary bladder** lies beneath the uterine body and in front of the vagina and the base of the urinary bladder is in contact with the anterior vaginal wall. Discuss the obstetrical significance of this close relationship with colleagues and your tutor.

2. Discuss the axes of the birth canal with colleagues and your tutor. Note that the birth canal is initially directed towards the **coccyx** (i.e. along the cervical axis), and turns inferiorly at the level of the cervical opening and upper vagina to pass down the vaginal axis. What would happen if the fetal head continued along the cervical axis?

3. Using the female pelvic model with ligaments, identify the **ischial spines**, **sacral promontory** and **subpubic angle**. Discuss with colleagues the possible effects of excessive prominence of the ischial spines or sacral promontory on the birth canal. Note the size of the subpubic angle in female and male pelves. It is around 80 to 90^{o} in females and about 60^{o} in males. Why is this angle significant during birth? Identify the **sacrotuberous** and **sacrospinous** ligaments. Discuss the importance of these ligaments and other factors in turning the fetal head as it enters the vagina.

4. With colleagues examine the fetal head, identifying the **frontal**, **parietal** and **occipital** bones. Note the presence of **sagittal**, **coronal** and **lambdoid** sutures between these bone plates. Identify the **anterior** and **posterior fontanelles** **(**position of **bregma** and **lambda** points, respectively**)**. When will these close up? What is the obstetrical significance of the loose sutures between the plates of the fetal skull? With colleagues try to determine the smallest dimension of the fetal skull which could be presented to the birth canal. Compare **suboccipitobregmatic** and

fronto-occipital dimensions. How might the fetal head be flexed or turned during birth to take advantage of the smallest skull dimension?

5. With colleagues and your tutor discuss the movement of the fetal head through the female pelvis, noting rotational movements of the fetal skull to take advantage of the largest dimensions of the pelvis at each level. Discuss the three stages of labour: first stage – dilation of the uterine cervix, second stage – movement of the fetal head and trunk down birth canal, and third stage – delivery of the placenta.

6. Most human infants are delivered with the **occiput** (back of the head) facing to the front of the woman, but in primates and other mammals the fetal occiput usually faces the mother's tail. What is the significance of this difference both obstetrically and culturally?

7. With colleagues and your tutor discuss the biological and cultural significance of the prolonged period of postnatal brain growth in human infants. What is happening in the infant's brain during the first few years after birth? Why is it difficult to remember anything which happened to us before the age of three? How has human culture adapted to the prolonged dependency of human infants? How has our species made use of this neonatal immaturity?

Practical 5 The human hand and tool use -- Part 1: Film Clips of Tool making

Specific Objectives:

1. To describe the different types of tool cultures from the lower and middle paleolithic and discuss the likely techniques for making those tools.
2. To define the differences between Middle and Upper Palaeolithic tools, indicating the greater variety and versatility of the latter.
3. To be able to discuss what the types of tools used by Upper Palaeolithic peoples tell us about their lives.

Learning Activities:

Casts of stone tools and film clips from you-tube will be shown to illustrate the following tool making summary. The different approaches in these clips suggest how tools from different technologies could have been made using techniques learned from trial and error by experimental anthropologists. The uses for these tools have been inferred from modern cultures that use similar tools today and the study of residues and microwear on original stone tools that have been found. Human technologies will be compared with those of other primates.

Tool cultures from the Lower and Middle Paleolithic and likely techniques for making those tools

Oldowan technology is the oldest known, dating from the Late Miocene (from 2.4 mya, named after the old name for Olduvai Gorge). It is exemplified by "**hand choppers**", which were originally thought to be the actual tool, but may really be the core material from which finer stone flakes were struck. The nodules found in early sites at Olduvai (1.2 to 1.8 mya) are flaked on one side only (i.e. unifacially). This can be done by striking one stone (the **hammerstone**) against another (the **core**) in a method called **direct percussion**. Later Oldowan technology (circa 0.4 mya) are flaked on two faces and have long sinuous edges. Such a result cannot be produced by direct percussion with just a hammerstone. The edges must have been retouched or straightened with a soft hammer, such as a bone or antler. Oldowan technology is associated with robust australopithecines and *Homo habilis*.

Acheulean technology is found in sediments dating from 0.12 mya to 0.7 mya, although some examples have been found in Africa dating as early as 1.4 mya. It has been associated with *H. erectus* and early archaic *H. sapiens*. The Acheulean technology saw the development of a core worked on two sides called a **biface** (known widely as a **hand axe** or cleaver). The biface had a flatter core than the roundish earlier Oldowan pebble tool. The biface core tool was obviously the <u>target design</u> rather than just the product of removing outer flakes from a pebble. The biface became the standard all-purpose Acheulean stone tool for a million years. It served to cut scrape, pound and dig. Towards the end of the Acheulean industry, toolmakers blocked out a core with stone hammers and then switched to wood or bone for refining the edges. This technique produced more elegant, pear-shaped tools.

Mousterian technology (40,000 to 125,000 years ago) is often (but not always) associated with Neandertals. Early modern humans from Israel also used this technology. In the early part of the last glacial period, Mousterian culture extended across Europe and North Africa into Uzbekistan and Iran. Neandertals produced flakes by trimming a flint nodule around the edges to produce a disk shaped core. Each time they struck the edge, they produced a flake, continuing this way until the core became too small and was discarded. The flakes were then retouched into various forms such as side scrapers, points and knives. Spears made of wood have also been found associated with Neandertal remains, but these may have been stabbing or short range throwing spears.

Upper Palaeolithic tools. What do they tell us about the people who used them?

There are many different tool technologies from the Upper Palaeolithic (10,000 to 40,000 years ago) because this was a period of rapid advance. Tools from the Upper Palaeolithic are different from earlier cultures in several ways:

- They show much more sophisticated workmanship. Pressure flaking techniques were developed and used to make beautiful parallel sided lance heads. The punch-blade technique allowed the manufacture of an abundance of standardised blank stone flakes. These could be fashioned into burins for working wood, bone or antler, borers for drilling holes in skins, bones or shells, and blades for knives with serrated or notched edges for scraping wooden shafts into a variety of tools.
- They often use combinations of materials (e.g. bone, sinew and wood, or wood and ivory).
- They may also have served as works of art or cultural symbolism. Some stone tools dating from this period were so delicate that they would have broken in ordinary use. Even utilitarian tools were decorated by carvings.
- They represent significant technological advances e.g. the atlatl or woomera, harpoons, sewn clothing.
- The first experimentation with fired pottery has been reported to date from this period (small animal figures from two sites in the Czech Republic dated at 27,000 years ago).

Tool making by other primates. Do you need a modern human hand to be a stone tool user and tool maker?

In the wild chimpanzees use crushed or chewed leaves as sponges to soak up drinking water trapped in tree branches and they strip the leaves from twigs to fish for ants or termites from their nests. They also use stone as a tool to crack nuts with cultural differences in their technology. Some groups use a wooden hammer on a stone anvil while others use a stone hammer on a stone anvil. It takes around 7-8 years for juveniles to learn and start to master this technique from observation and trial and error. Stones can also be used as a weapon.

Culturally based, stone tool using behavior is not confined to apes. Some monkey troupes in South America bring nuts to a communal flat stone to use as the anvil, where they crack them open with stones as the hammer.

Bonobos and other apes in captivity have been shown stone tool making to make a sharp flake from a core. Successfully using this technology shows the ability to intentionally and skillfully make functional knives and manipulate them to cut rope.

Practical 5 The human hand and tool use -- Part 2: Laboratory

Specific Objectives:

1. To be able to identify the major bones and muscles of the human hand (see learning activities).
2. To demonstrate precision and power grips and indicate when each would be used. To be able to demonstrate opposition of the thumb with the other digits and indicate the functional significance of this movement.
3. To discuss the functional significance of the uniquely hominin features of the hand (1st carpometacarpal joint), elongated and rotated thumb, development of thenar and hypothenar muscles.
4. To indicate the functional significance of two point discrimination and dermatoglyphs in the human hand.
5. To be able to identify representative stone tools from selected paleolithic cultures (Oldowan, Acheulean, Mousterian, Solutrean) and indicate which hominins these tools are associated with.

Learning Activities:

1. Using human bones and articulated skeletons identify the bones of the hand (**carpals** as a group, **metacarpals**, **proximal**, **middle** and **distal phalanges**). Note the joint between the end of the **radius** bone of the forearm and some of the carpal bones (in particular, the **trapezium** and **scaphoid** at the base of the thumb). Note also the ability of the radius to rotate around the long axis of the forearm. This allows a pair of movements called **pronation/supination** depending on the direction of rotation. Pronation is the movement which allows one to lay the <u>palm</u> face down on a table, while supination is the rotation allowing the <u>back</u> of the hand to lie flat on a table. What common type of modern tool use depends on rotation of the forearm? Identify muscles that produce pronation (**pronator quadratus** and **pronator teres**) and supination (**biceps brachii**, **supinator**) and observe how their fibre orientation allows these actions.

Note the special nature of the joint (**1st carpometacarpal joint**) between the proximal phalanx of digit 1 and the **trapezium bone** (one of the carpals) in modern humans. This joint surface has a saddle-shape that allows flexion/extension and abduction/adduction, but restricts rotation around the metacarpal long axis. Examine this joint in the gorilla or chimp.

2. Identify the muscles of the forearm associated with bending (flexion) of the fingers and straightening (extension) of the fingers. What sort of grip would the **forearm flexors** be involved in? Note that forearm flexors are divided into superficial (close to skin surface; **flexor digitorum superficialis**) and deep groups (**flexor digitorum profundus**) and that these two groups of muscles have different actions on the finger joints. Identify the **extensor digitorum** muscle. Note that one of the **forearm extensors** is specifically concerned with straightening the index finger alone, i.e. in isolation from the other fingers. This is called the **extensor indicis**. Why would this muscle be useful both in modern society and for ancient humans?

3. Identify the intrinsic muscles of the hand. Many of these are grouped into muscular pads at the bases of the thumb and little finger, called **thenar** and **hypothenar eminences**, respectively. The thenar eminence includes **opponens pollicis**, **flexor pollicis brevis** and **abductor pollicis brevis**. The hypothenar eminence includes **opponens digit minimi**, **flexor digiti minimi brevis** and **abductor digit minimi**. Other intrinsic muscles lie between the metacarpals

(**interosseus** muscles and **lumbricals**). Using movements of the digits of your own hand, deduce the functions of the intrinsic muscles. How are precision translation movements made?

4. With colleagues and your tutor, practice different movements of the hand (**power grip**, **precision grip**, **opposition** of the thumb with other digits, **divergence** of fingers, **convergence** of fingers). Identify examples of **hook grip** (holding a shopping bag), **pinch grip** (holding a key to insert into a door lock), **precision translation** (threading a needle) and **precision rotation** (rotating a small screwdriver or small knob) and briefly consider the muscles involved in each. Which muscle groups are involved in these hand movements?

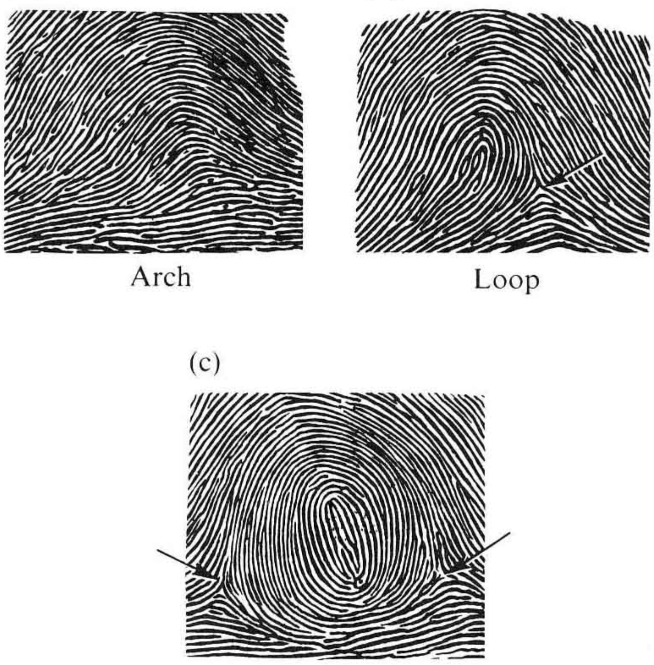
5. With colleagues and your tutor, discuss the major structural differences between the human and ape hand. Note the length and orientation of the thumb and relative development of thenar and hypothenar musculature.

Study illustrations of hominin hand bones: Do these hominin hands resemble human or ape hands?

Now hold your thumb flexed at the joint between the proximal and distal phalanx. Use the medial side of the proximal phalanx to grip objects against the 2nd metacarpal. How much harder is this than a human precision grip?

	Homo sapiens	*Pan paniscus* (bonobo)	*Gorilla gorilla*
Width of digit 1 distal phalanx tip/pad (a)			
Length of digit 1 distal phalanx (b)			
Ratio b/a expressed as *x*:1			
Shape of surface of 1st carpometacarpal joint surface			

6. Look closely at the skin of your finger pads (and those of colleagues). Compare with the sets of fingerprint images provided and the figure below showing three types of human finger print (**arch**, **loop** and **whorl**). The arrows point to a region known as the **triradius**. Try to identify the three different types of fingerprint on your digits or those of a colleague. How might fingerprints contribute to the functional capacity of the hand?


(a) Arch (b) Loop (c) Whorl

7. An important functional aspect of the human (and primate) hand is its enhanced sensitivity relative to other parts of the body. With colleagues use the tooth-pick pairs provided to test on a volunteer for **two-point discrimination.** This is the ability to determine whether one has been touched by a single point or two points very close together. Test two point discrimination (i.e. the closest distance between two points that can still be distinguished) on the **abdomen**, **sole of foot**, **scalp**, **arm**, **palm of hand**, **thumb pad**. Which part of the body has the smallest value? What is the functional significance of this? What features in the skin might contribute to this sensory difference between regions? What other types of sensory function might be useful in a tool-using hand? How do you assess the texture (i.e. smoothness vs roughness) of those objects you touch?

8. Examine models of representative lower and middle Paleolithic (**Oldowan**, **Acheulean**, **Mousterian**) stone tools. Note the progression in delicacy and refinement of workmanship in these different tool cultures. With colleagues and your tutor discuss probable techniques used by hominins in making these tools. Try to deduce the possible use of each tool. How would you experimentally confirm the actual use made of a particular tool? Might some of these tools have had importance to ancient hominins apart from their practical value?

9. Examine examples of upper Paleolithic and Neolithic stone tool technology. Discuss core and flake technology and polished stone tools and how these are made.

Practical 6 The human brain

Specific Objectives:

1. To identify the major parts of the hominin brain and assign broad functions to each.
2. To define the concept of functional areas in the cerebral cortex and indicate the positions of the major functional areas.
3. To be able to describe techniques for making cranial endocasts and indicate the sort of information which can be obtained from these casts.
4. To be able to identify gross anatomical features of the hominin brain using illustrations of hominin cranial endocasts.

Learning Activities:

1. Using models and specimens of the human brain identify the main parts of the brain (**medulla**, **pons**, **midbrain**, **cerebellum** divided into **vermis** and **cerebellar hemispheres**, **diencephalon** divided into **thalamus** and **hypothalamus,** and **cerebral cortex**). Discuss the broad functions of each of these parts with colleagues and your tutor and complete the table below. Recall that the cerebral cortex occupies about two-thirds of the human brain volume. Note the extensive folding of the cerebral cortex (**gyrification**). What is the significance of this folding? Note the presence on the medial surface of the cerebral hemisphere of a large fibre bundle of about 300 million myelinated axons called the **corpus callosum**. This joins the two cerebral hemispheres and allows ready transfer of information from one side to the other. What functional implications might the existence of this bundle have for brain evolution? How might its enlargement contribute to functional asymmetry of the hominin brain?

Brain part	**Function**
Medulla	
Pons	
Midbrain	
Cerebellum vermis hemisphere	
Diencephalon - thalamus - hypothalmus	

- pituitary gland - pineal gland	
Cerebral cortex	

2. The cerebral cortex is broadly divided into **frontal**, **parietal**, **temporal** and **occipital lobes**. Discuss the idea of functional areas of the cerebral cortex with colleagues and your tutor. How were these functional areas discovered? Using models and human brain specimens identify the **primary motor** and **somatosensory cortices**. Note that these regions are separated by a prominent groove called the **central sulcus**. How are different parts of the body represented along these cortical regions? Identify the **primary visual cortex** at the back of the brain. This region is very large in humans but only a small part of it is visible on the outside of the brain – much of the primary visual cortex lies deep within a groove called the **calcarine fissure**. The **primary auditory area** lies on the upper surface of the **temporal lobe** of the brain, extending into another very deep groove called the **lateral fissure**. **Olfactory cortex** is located on the medial surface of the temporal lobe. Discuss with colleagues and your tutor how aspects of two senses (vision and hearing) might be organized in these two cortical sensory areas (**visuotopic** and **tonotopic organization**).

3. Much of the human cerebral cortex is taken up by regions concerned with so-called "higher functions". For example, the area in front of the motor cortex is called the **prefrontal cortex** and is concerned with planning, working memory and social behaviour. How would development of this region have been important for early hominins? Another area between the visual, auditory and somatosensory cortices is called the **parietal/temporal/occipital association cortex** (**PTO cortex**). It is concerned with integrating, or bringing together, information from all three senses to form a complete picture of the outside world. Discuss the importance of this brain region for the life of early hominins. Regions in the temporal lobe are concerned with memory, facial recognition and emotions. What is the social importance of these? Identify the **hippocampus** and **amygdala** inside the temporal lobe and the **fusiform or occipitotemporal gyrus** (facial recognition area) on the underside of the temporal lobe.

4. With colleagues and your tutor, discuss techniques for making cranial endocasts. What sort of information can be obtained from cranial endocasts? Might it be possible to identify functional cortical areas in cranial endocasts of fossils? What features often outline functional areas in modern humans? What would be the limitations of such interpretations of fossil material?

5. Using the endocast model and illustrations of natural and artificial cranial endocasts, look for impressions of some of the same gross anatomical features which you have seen on the modern human brain. Try to identify the **lateral fissure**, **central sulcus**, **temporal lobe**, **parietal lobe**, **occipital lobe** and **frontal lobe**. Would the calcarine fissure ever be visible on a cranial endocast?

6. The brain and perception: different viewpoints. It is easy to study the physical brain and even its electrical activity. It is very difficult to study the processes of perception, interpretation and thoughts in individuals. Not everyone thinks in the same way so it is probably incorrect to assume human development occurred according to particular patterns of thinking and perception of the world. This is especially true in relation to theories on the origin of language, cultural development and humanity.

This can be illustrated by two examples of famous people with totally different perspectives on the same world we all think we know.

Temple Granden is a world expert on the behaviour of livestock and the design of handling practices and equipment. She is also autistic. She acknowledges that her perception of the world is different because her sensory perception is different. She expressed amusement on reading that hominins needed to develop language in order to develop culture and a tool technology. She was an adult before she found out that other people think linguistically. She has always thought in pictures and cannot conceive of any other way of thinking, yet her career is built on the design of technology and teaching.

A famous horse whisperer (upon whom the novel by Nicholas Evans was based) is colour blind and so sees the world like a wolf rather than a primate. His vision is well suited to detecting movement at long distances and under low light conditions. He has spent many hours watching wild horse herds from afar and picked up on their non-verbal communication. He regularly teaches people to coerce wild horses to accept a man in a saddle in 30 minutes, using their language signals. This is a skill no other horse trainer has developed. Our anthropocentric view of the world has made it hard for us to accept and see communication in other species.

Practical 7 The human face and the functional anatomy of language – Part 1: Films on Ape/Human Brain Function and Facial Communication

Practical 7 The human face and the functional anatomy of language – Part 2: Laboratory

Specific Objectives:

1. To identify the major facial muscles involved in human facial expression and identify the parts of the cerebral cortex involved in facial motor control and somatosensation.
2. To identify the major structural features of the larynx, pharynx, tongue and palate, indicating how the sounds of human speech are produced in the larynx and modified by alteration of the column of air above the larynx.
3. To identify the language areas in the brain (Broca's and Wernicke's) and the pathway connecting them (arcuate fasciculus). Indicate, using examples from clinical neurology, the importance of these regions in human language.

Learning Activities:

1. Using specimens of the human face identify the following facial muscles: **orbicularis oculi**, **orbicularis oris**, **frontalis**, **buccinator**, **zygomaticus major and minor**. Also identify the fine nerve branches distributed to these muscles (**facial nerve**) as it emerges from the parotid gland. Discuss with colleagues and your tutor the roles of these muscles and indicate the types of facial expressions which they produce.

2. Using models and half brains, identify the **primary motor** and **somatosensory cortices** indicating the regions within each associated with the human face. Why does the human cerebral cortex have such a large representation for facial structures? Which particular parts of the face are represented the most and why?

3. Examine a sagittally sectioned head and neck specimen to identify the **larynx**, **pharynx**, **oral cavity** and **nasal cavity**. Note that the pharynx can be divided into three regions, e.g. behind the nasal cavity (**nasopharynx**), oral cavity (**oropharynx**) and larynx (**laryngopharynx**), respectively. The nasal cavity is separated from the oral cavity by the palate, which can be divided into bony (**hard palate**) and muscular (**soft palate**) parts. The floor of the oral cavity is filled by the **tongue**, a large mobile muscular structure, which is attached to the floor of the mouth at the back of the oral cavity. Using a model of the tongue note that muscles within this structure (**intrinsic musculature**: **longitudinal**, **transverse** and **vertical**) can readily alter its shape, while muscles connecting the tongue to nearby structures (**genioglossus**, **hyoglossus**, **palatoglossus** and **styloglossus**) can move the tongue in all three spatial dimensions.

4. Study the model of the larynx, noting that this structure consists of a "skeleton" of cartilages (**thyroid**, **cricoid** and **arytenoid**) covered by muscles and mucous membranes. Note also the **hyoid bone** below the mouth and above the larynx. This bone provides an important attachment for muscles of the throat and

tongue and reinforces the upper airway, preventing collapse during deep inspiration. Note the paired **vocal folds**, which are produced by mucous membranes laid over the vocal ligaments. These can be brought together or moved apart by rotation of the arytenoid cartilages. Note also that the airway to and from the lungs (the **trachea**) begins immediately below the larynx. The vocal folds vibrate to produce the voice. How does this occur? Discuss with colleagues the mechanical factors which could alter the pitch (frequency) of the voice. How do movements of laryngeal cartilages produce different voice frequencies?

5. Discuss with colleagues and tutors the changes, which occur in the upper airway and oral cavity to produce vowels and consonants. What is the difference between the two? How can consonants be classified according to their site of production (e.g. labial – p, b; dental – t, d; nasal – m, n; glottal – g, k)? What movements of tongue, soft palate and pharynx occur with each type?

6. Study the human left cerebral hemisphere and indicate the positions of **Broca's** and **Wernicke's** areas. Broca's area occupies the **triangular** and **opercular pats of the inferior frontal gyrus**. Wernicke's area usually occupies a flattened region on the upper surface of the temporal lobe known as the **planum temporale,** but can also extend into the **angular** and **supramarginal gyri** of the **inferior parietal lobule**. In dissections of the underlying white matter note the **arcuate fasciculus**. What are the functions of each of these structures? Why are they usually found in the left cerebral hemisphere? What relationship exists between the side on which language areas lie and other aspects of neurological function (e.g. handedness)? Are these regions present in other primates? Does cerebral asymmetry exist in other mammals?

Tutorial 1 Group orientation and choosing laboratory project topics

The purpose of this initial tutorial is to bring you together and allow you to form subgroups to work as a team on the laboratory project.

- For the project you should work in teams of 3 to 4 students.
- All students in the group will receive the same mark for the project, so you should work together as a team.
- You will be expected to research the topic and prepare laboratory work, the laboratory project report and an accompanying 15 minute oral presentation for the final tutorials. There will be a 5 minute question time for each group.
- <u>All</u> team members must contribute to the lab project work, report and oral presentation.
- At the final presentation you will be asked to indicate the contributions made by team members.
- Sample assessment sheets are provided at the end of the course notes.

Laboratory projects:

All laboratory projects incorporate: i) a research component (acquiring and reading the relevant literature; ii) a practical component (reconstruction of musculature and/or other soft tissue using coloured plasticene); iii) preparing a written report explaining the functional implications of the reconstruction; and iv) an oral report to fellow students on the findings.
All reconstructions should be as anatomically accurate and neat as possible, allowing distinction to be made between key structures in the reconstruction. Skin covering is not necessary.

The models are property of the School of Medical Sciences and must NOT be damaged during the project. All plasticene must be removed from the model at the end of the project.

1) **Reconstruction of the foot of a great ape**
The aim of this project is to use a model of the skeleton of the foot (pes) of a great ape to reconstruct the musculature of the foot of that great ape and to compare this with the musculature of the modern human foot.
The key questions that you should address are:

- How does the musculature of the pes of your great ape differ from modern humans?
- How do the differences in skeleton, joints and musculature between apes and humans affect the function of the pes?

2) **Reconstruction of the facial soft tissues of a great ape**
The aim of this project is to use a model of the skull of a great ape to reconstruct the musculature of the face of that great ape and to compare this with the musculature of the modern human face. You may use models of robust chimpanzee, bonobo or orangutan as your model, so more than one group may do this project topic.
The key questions that you should address are:

- How do the hard and soft tissues of the face of your great ape differ from modern humans?

- How do the shape of the facial skeleton and arrangement of facial musculature affect the facial expressions available to your ape?

3) **Reconstruction of the hand of a great ape**
The aim of this project is to use a model of the skeleton of the hand (manus) of a great ape to reconstruct the musculature of the manus of that great ape and to compare this with the musculature of the modern human manus.
The key questions that you should address are:

- How does the musculature of the manus of great apes differ from modern humans?
- How do differences in skeleton, joints and musculature between apes and humans affect the function of the manus?

4) **Reconstruction of the pelvic floor and contents of a great ape**
The aim of this project is to use a model of the skeleton of the pelvis of a great ape to reconstruct the pelvic floor musculature and internal pelvic organs of that great ape and to compare this with the musculature and internal organs of the modern human pelvis.
The key questions that you should address are:

- How does the skeleton and musculature of the pelvis of great apes differ from modern humans?
- How do differences in skeleton, joints and musculature between apes and humans affect the anatomy of the birth canal?

5) **Reconstruction of the facial soft tissues of *Homo habilis***
The aim of this project is to use a model of the skull of *Homo habilis* to reconstruct the musculature of the face of that hominin and to compare this with the musculature of the modern human face.
The key questions that you should address are:

- How do the hard and soft tissues of the face of *Homo habilis* differ from modern humans?
- How does the shape of the facial skeleton and arrangement of facial musculature affect the facial expressions available to your hominin?

6) **Reconstruction of the facial soft tissues of *Homo sapiens neanderthalensis***
The aim of this project is to use a model of the skull of *Homo sapiens neanderthalensis* to reconstruct the musculature of the face of that hominin and to compare this with the musculature of the modern human face.
The key questions that you should address are:

- How do the hard and soft tissues of the face of *Homo sapiens neanderthalensis* differ from modern humans?
- How does the shape of the facial skeleton and arrangement of facial musculature affect the facial expressions available to your hominin?

7) **Reconstruction of the soft tissues of the vocal tract of *Homo sapiens neanderthalensis***
The aim of this project is to use models of the skull and hyoid bone of *Homo sapiens neanderthalensis* to reconstruct the musculature and other soft tissue of the larynx and pharynx of that hominin and to compare this with the modern human larynx and pharynx.
The key questions that you should address are:

- How do the hard and soft tissues of the throat of *Homo sapiens neanderthalensis* differ from modern humans?
- How does the shape of the vocal tract affect the range and quality of vocalisation and articulation available to your hominin?

Requirements for the project report:

- The report must clearly indicate the student identification numbers of all group members on the title page.
- The report should be divided into the following sections: title page; table of contents; introduction; body of report; summary of conclusions; references.
- Do not exceed the allowed report length of 2,500 words (excluding references and figure legends).
- Information in the text should be supplemented and supported by visual media, i.e. relevant photographs, diagrams, tables or graphs. All forms of visual media must have figure legends.
- Showing evidence of critical thinking about the topic will earn higher marks. This should include a thoughtful consideration of the quality of evidence for contentions in the literature.
- Provide references to scientific and other sources using the Harvard (name, date) system.

Tips for oral presentation

- Introduce the group members and briefly explain the contribution of each.
- Each group member must make a contribution to the oral presentation. Practice together.
- Be expressive. Change pace and intonation. Do not speak too quickly.
- Maintain eye contact with the audience.
- Try to avoid use of written notes or excessive use of palm cards. You should all practice your talk so that it can be delivered from memory.
- Practice with an outsider so that you get insight into what is difficult for a naïve person to understand.
- Keep to the time. Marks will be deducted for overlong presentations.
- Show enthusiasm for the topic.
- Ask for questions at the end. Answer clearly and to the point.

Tutorial 2 and 3 Presentation of laboratory projects

ıents:

Project Report: Staff Assessment

Project Title:……………………………………………………………

Assessor:………………………………………..

1. Title: The quality of language was:	Marks
• appropriate and professional	☐ 4
• clearly expressed, reasonably readable and fairly informative	☐ 3
• difficult to read and/or somewhat uninformative	☐ 2
• poorly expressed, uninformative and/or vague	☐ 1
2. Structure: The sequence of material in the report was:	
• clearly structured and very easy to follow	☐ 4
• reasonably clear, fairly easy to follow	☐ 3
• somewhat unclear, not easy to follow	☐ 2
• unclear and difficult to follow	☐ 1
3. Illustrations and summary tables were used:	
• to excellent effect, appropriately sized and legible	☐ 4
• to good effect, reasonable size and legibility	☐ 3
• to poor effect, small size/not clear/marginal relevance	☐ 2
• ineffectually, not relevant/poorly presented	☐ 1
4. Content: The level of information presented was:	
• excellent – neither too general nor too detailed	☐ 4
• good – mostly appropriate but could be improved	☐ 3
• poor – too general or inappropriately detailed	☐ 2
• inappropriate – far too general	☐ 1
5. Referencing and critical analysis: The use of sources was:	
• excellent, with abundant evidence of critical thinking	☐ 4
• good, with some evidence of critical thinking	☐ 3
• poor, with minimal evidence of critical thinking, errors in references	☐ 2
• very poor, with insufficient and inaccurate referencing	☐ 1

Report Mark /20 =

Comments:

Group Oral Presentation: Staff Assessment

Project Title Presented:………………………………………………………………

Date:……………….. **Tutor**:………………………………………..

1. The speaker/s were clearly audible, maintained eye contact with listeners and did not read directly: Marks
   - throughout the talk ☐ 4
   - for most of the talk ☐ 3
   - for little of the talk ☐ 2
   - hardly ever ☐ 1
2. Speakers referred to the model/additional material to illustrate key points:
   - frequently ☐ 4
   - regularly ☐ 3
   - rarely ☐ 2
   - hardly ever ☐ 1
3. Structure and organisation of the talk were:
   - very clear with distinct introduction, content and conclusions ☐ 4
   - fairly clear, if a little confused at times ☐ 3
   - unclear ☐ 2
   - very poorly organised ☐ 1
4. Content of the talk compared to the written report:
   - complemented text well, excellent relevant additional information ☐ 4
   - mostly complemented the text, reasonable additional information ☐ 3
   - mostly repeated the information in text, some additional information ☐ 2
   - merely repeated the text ☐ 1
5. Critical analysis of the topic/paper:
   - excellent ☐ 4
   - good ☐ 3
   - poor ☐ 2
   - very poor ☐ 1

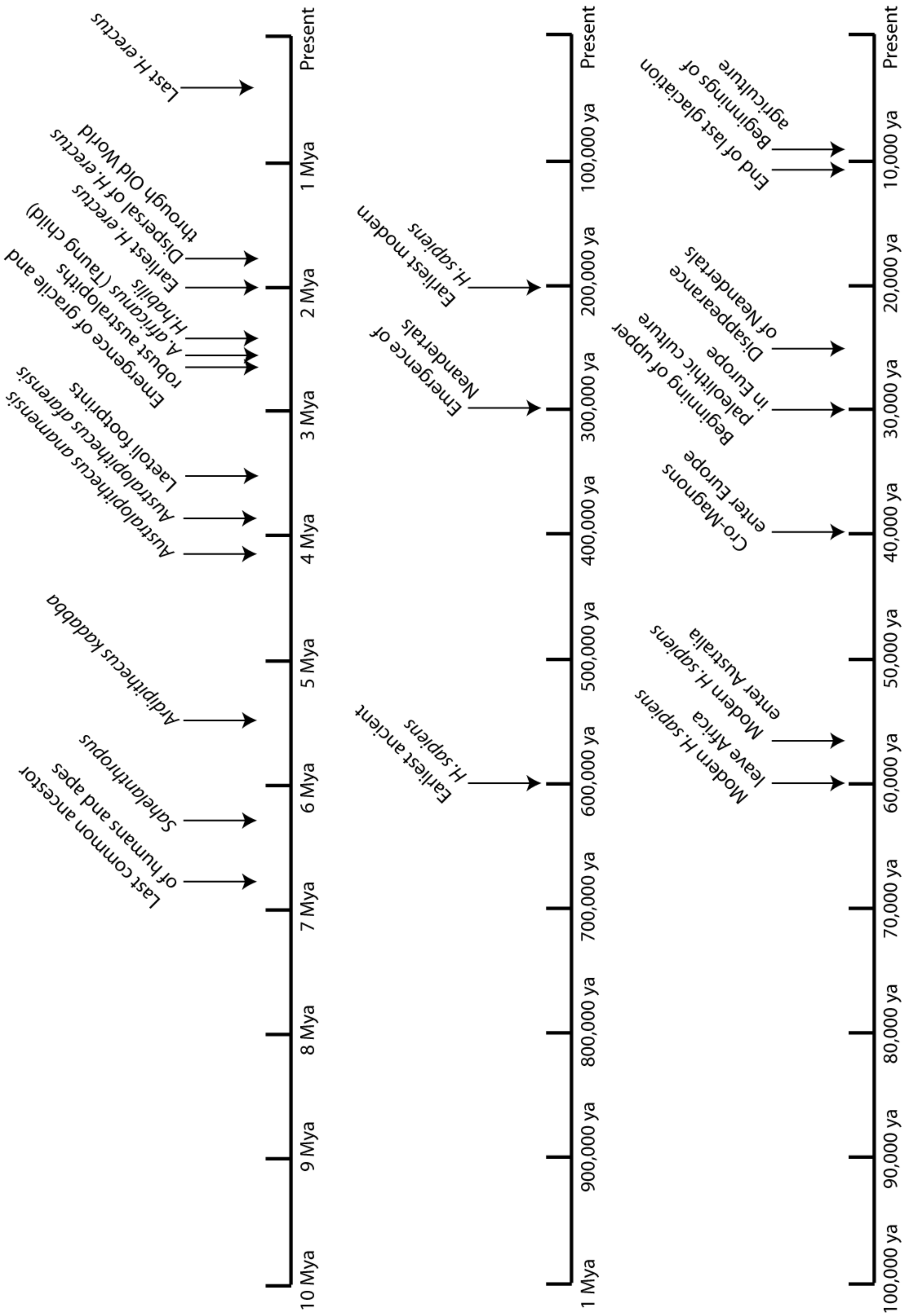
Presentation Mark /20 =

Point Summary of Evolution

- All organisms have common ancestry, the so-called evolutionary tree.
- Species gradually change as ecosystems (environments) change. New species emerge whilst others become extinct.
- Evolutionary processes act on populations by affecting the reproductive outcomes of individuals. The fittest individuals have the most offspring.
- The major mechanisms for change affect gene frequencies within the population. These include: natural selection, migration, inbreeding, random genetic drift[1], and founder effect[2].
- The form of an organism is the best compromise for the environment at a particular time. The more specialized ("perfect") the organism, the more susceptible it is to extinction because of its inability to adapt to sudden environmental change.
- The evolutionary pathways observed in the fossil record were **not** inevitable. If evolution were to occur again on this planet, the results would not necessarily be the same.
- Evolution is not hierarchical. Humans are not the pinnacle of the evolutionary process.
- Evolution is not linear. The fossil record contains evidence of ancestral forms of plants and animals which are not directly related to modern species. In the case of human evolution, several different species were known to have coexisted at the same time, one or none of which may have been the human ancestor.

[1] allele frequencies are subject to probability, not selection, in very small populations

[2] a small starter population has only a limited subset of the genetic variability of the parent population


Present
1 Mya
2 Mya
3 Mya
4 Mya
5 Mya
6 Mya
7 Mya
8 Mya
9 Mya
10 Mya
Last H.erectus
Dispersal of H.erectus through Old World
Earliest H.erectus
H.habilis
A.africanus (Taung child)
Emergence of gracile and robust australopiths
Laetoli footprints
Australopithecus afarensis
Australopithecus anamensis
Ardipithecus kadabba
Sahelanthropus
Last common ancestor of humans and apes
Present
100,000 ya
200,000 ya
300,000 ya
400,000 ya
500,000 ya
600,000 ya
700,000 ya
800,000 ya
900,000 ya
1 Mya
Earliest modern H.sapiens
Emergence of Neandertals
Earliest ancient H.sapiens
Present
10,000 ya
20,000 ya
30,000 ya
40,000 ya
50,000 ya
60,000 ya
70,000 ya
80,000 ya
90,000 ya
100,000 ya
Beginnings of agriculture
End of last glaciation
Disappearance of Neandertals
Beginning of upper paleolithic culture in Europe
Cro-Magnons enter Europe
Modern H.sapiens enter Australia
Modern H.sapiens leave Africa