

12

TRENDS IN HOMINID EVOLUTION

UNIT 4 CONTENT

SCIENCE INQUIRY SKILLS

- » conduct investigations, including the use of virtual or real biotechnological techniques of polymerase chain reaction (PCR), gel electrophoresis for deoxyribonucleic acid (DNA) sequencing, and techniques for relative and absolute dating, safely, competently and methodically for valid and reliable collection of data

SCIENCE UNDERSTANDING

Hominid evolutionary trends

- » humans as primates are classified in the same taxonomic family as the great apes. The species within the family are differentiated by DNA nucleotide sequences, which brings about differences in:
 - relative size of cerebral cortex
 - mobility of the digits
 - locomotion – adaptations to bipedalism and quadrupedalism
 - prognathism and dentition

Source: School Curriculum and Standards Authority,
Government of Western Australia

12.1 HUMANS AS PRIMATES

Humans, apes, monkeys and some other related animals are called primates because they are all classified together in the taxonomic order Primates. The non-human primates are of special interest to us because they are the closest living relatives of our own species. A comparative study of primates is fundamental to any investigation of the evolution of modern humans. In trying to develop an understanding of how human characteristics evolved, a number of sources of evidence can be used:

- comparative anatomy
- comparative biochemistry, including DNA and proteins
- behaviour of living primates
- fossils of primates.

Humans are classified in the same family as the great apes: chimpanzees, bonobos, gorillas and orangutans. The great apes share the most recent common ancestor with humans and, therefore, share many of our characteristics, including very similar DNA.

CLASSIFICATION GROUP	EXAMPLES
Order Primates	Humans, apes, monkeys, tarsiers, lorises and lemurs
Suborder Haplorrhini	Humans, apes, monkeys and tarsiers
Infraorder Simiiformes	Humans, apes and monkeys
Superfamily Hominoidea	Humans and all apes (great apes and gibbons)
Family Hominidae	Humans and great apes
Subfamily Homininae	Modern and extinct chimpanzees, gorillas and humans
Genus <i>Homo</i>	Modern and extinct humans
Species <i>sapiens</i>	Modern humans

FIGURE 12.1 Diagrammatic representation of the hierarchy within the Primate order

TABLE 12.1 Classification of humans within the Primate order

LEVEL OF CLASSIFICATION	NAME	EXAMPLES
Order	Primates	Primates include tarsiers, lemurs, lorises, monkeys, apes and humans
Suborder	Haplorrhini	Haplorrhini include tarsiers, monkeys, apes and humans
Infraorder	Simiiformes	Simiiformes include monkeys, apes and humans
Parvorder	Catarrhini	Catarrhines include Old World monkeys, apes and humans
Superfamily	Hominoidea	Hominoids include apes and humans
Family	Hominidae	Hominids include all modern and extinct orangutans, gorillas, chimpanzees and humans





Humans are apes

This website explains why humans are apes.

Primate images

This website has some excellent photos of primates.

What is a primate?

This website provides more information about the characteristics of primates.

What makes a primate a primate?

This website describes what makes a primate a primate.



LEVEL OF CLASSIFICATION	NAME	EXAMPLES
Subfamily	Homininae	Hominines include all modern and extinct chimpanzees, gorillas and humans
Tribe*	Hominini	Hominins include extinct ancestors of humans and modern humans
Genus	<i>Homo</i>	<i>Homo</i> includes some extinct ancestors of humans and modern humans
Species	<i>sapiens</i>	<i>Homo sapiens</i> are modern humans

Note: *Tribe is a classification group within a subfamily. The meaning of 'tribe' here is different from its use to describe an ethnic group of people.

It is common for the term 'ape' to refer to gorillas, orangutans and chimpanzees, and not humans. However, as they are all in the same family, humans can also be considered apes.

Characteristics of primates

There is no one characteristic that can be used to separate the primates from all other mammals. However, some features shared by all primates can be used to identify them as a group. Most of these features are a result of primates having evolved in an arboreal, or tree-like, environment. Two of these, grasping fingers and toes and overlapping vision, when taken together are distinctive to the primates. Table 12.2 summarises the characteristics of primates.

TABLE 12.2 Summary of the characteristics of members of the order Primates

FEATURE	PRIMATE CHARACTERISTICS
Body	Not specialised for a particular environment
Limbs	Generally unspecialised
Hands/feet	Pentadactyl – five fingers or toes Nails instead of claws Grasping fingers and toes with friction ridges for gripping First digit opposable
Eyes	Forward facing for three-dimensional (stereoscopic) vision Most are able to distinguish colour
Sense of smell	Very poor
Teeth	Four incisors in both the upper and lower jaw
Brain	Large and complex Cerebrum size increases as primates become more highly evolved
Reproduction	Not restricted to a breeding season Rhythmical sexual cycle Usually only one offspring at a time Long period of parental care for offspring

Key concept

Humans, chimpanzees, orangutans and gorillas are primates that are classified as great apes.

Questions 12.1

RECALL KNOWLEDGE

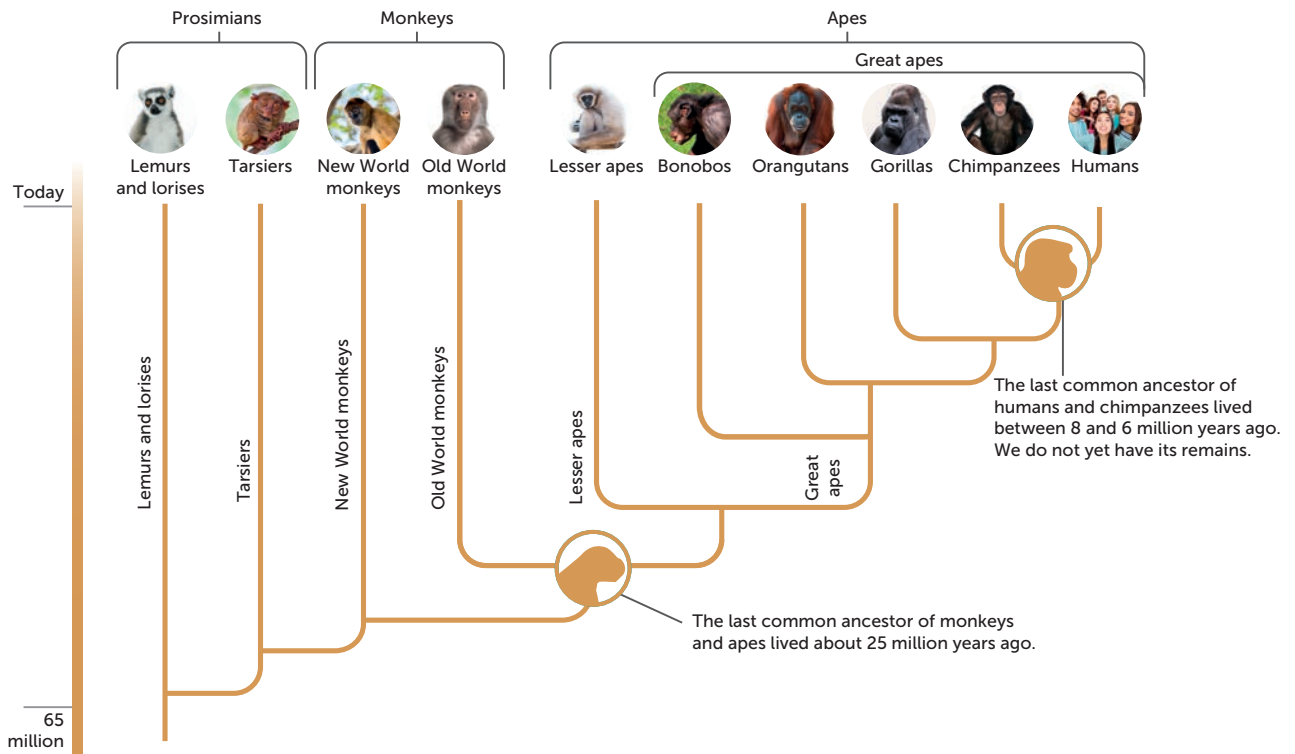
- 1 Monkeys, humans and gorillas are all in which taxonomic order?
- 2 Define 'arboreal'.
- 3 List five characteristics of all primates.

APPLY KNOWLEDGE

- 4 An unknown species is discovered. It has five fingers with claws, an opposable thumb and a small cerebrum that has limited convolutions. Would the species be classified as being a member of the family Hominidae? Explain your answer.

12.2 VARIATION WITHIN THE FAMILY HOMINIDAE

Humans are in the same family as the great apes (orangutans, gorillas, chimpanzees and bonobos). This family is called Hominidae, and its members are called **hominids**. Previously, only humans were classified in this family. However, advances in molecular techniques have shown that humans share a common ancestor with chimpanzees and gorillas. Orangutans and humans are slightly more distantly related, with bonobos separating at a more distant branch of the phylogenetic tree.



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FIGURE 12.2 Phylogenetic tree for primates

All species in the family Hominidae share some characteristics. These include:

- a larger, more complex brain than other primates. This enables an increased cognitive ability that means they can recognise themselves in a mirror
- five cusps in the molar teeth of the lower jaw
- arms that can freely rotate at the shoulder
- a wide, shallow chest cavity
- no external tail
- an appendix
- being active during the day (**diurnal**).

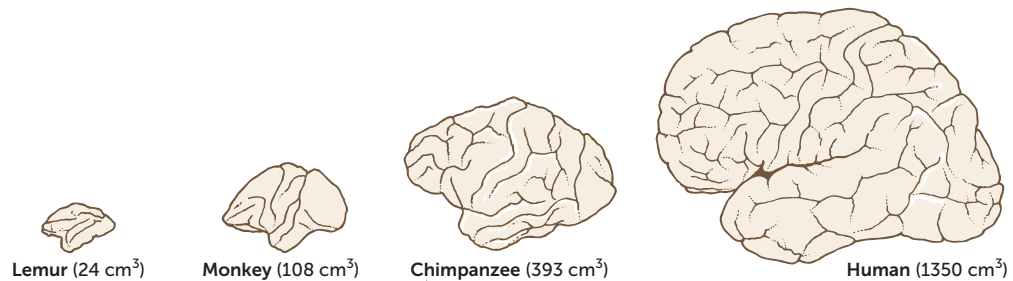
However, there are also some variations that reflect changes in the DNA nucleotide sequences during evolution. Some of these changes relate to:

- relative size of the cerebral cortex
- mobility of the digits
- locomotion – adaptations to bipedalism and quadrupedalism
- prognathism and dentition.

Changes in the relative size of the cerebral cortex

In the primates, the part of the brain responsible for complex functions, the **cerebrum**, has progressively increased in size. This is especially true of the outer region called the **cerebral cortex**. It is this region of the brain that is concerned with so-called higher functions – vision, memory, reasoning and manipulative ability. These functions are necessary to cope successfully with changes in the environment. Figure 12.3 illustrates the increase in size and complexity of the cerebrum from lemurs to humans. This is one of the most significant features of primate evolution.

FIGURE 12.3 The increase in size and complexity of the cerebrum in various primates (drawn to scale)



Primates have large brains for their body size. This seems to be a consequence of their tree-dwelling environment. The pressure of natural selection in an arboreal environment would have favoured more accurate visual and tactile perception along with better coordination between such sensory stimuli and any muscular response. Unlike smell or hearing, the reliance on vision to move about, and to locate and manipulate food, generates a large amount of complex sensory information that has to be processed and stored. In primate brains, such operations are carried out by the cerebral cortex. Progressive expansion of the cerebral cortex has resulted in it becoming so large that it covers the rest of the brain. This is most noticeable in humans.

Humans' brains range in size from 900 cm³ to 2200 cm³, but average around 1350 cm³ in adulthood. This contrasts markedly with those of the other apes, which average between 400 cm³ and 500 cm³. Most of the difference in brain size is associated with the cerebrum, especially the cerebral cortex.

Compared with other apes, the front part of the cerebrum, known as the **frontal lobe**, has the greatest enlargement in surface area. In humans it makes up 47% of the total cortical surface, whereas in apes it comprises only 33%. It is in the frontal lobe that the higher functions of thinking, reasoning, planning and processing take place.

The brains of hominids have a strong pattern of convolutions. These **convolutions**, or folds, enable the surface area of the brain, and hence the cerebral cortex, to be greatly increased. Notice how, in Figure 12.3, the cerebrum becomes larger and more convoluted as we progress from lemur to monkey, chimpanzee and human. These convolutions have resulted in a 50% increase in the surface area of the human brain compared with what it would be on a brain with no convolutions.

The increase in size of the cerebral cortex has had far-reaching effects on the way primates live. It has enabled them to move about and locate food, and to develop special skills. One of the most significant of these is tool making. This ability is most highly developed in humans, but is also seen in chimpanzees. Tool making, as opposed to tool use, involves a predetermined image of what the completed tool should look like – something only possible with a highly developed brain.



Primate brains

This website shows views of the brains of various primates and other mammals. Click on the particular species and then on the brain photographs to see an enlargement.

In addition, an increase in the size of the cerebral cortex would have allowed a greater variety of behavioural responses to meet a wide array of environmental problems. For most primate species, daily life involves numerous interactions with relatives, allies and adversaries. Mutual cleaning and grooming help to reinforce relationships, while threats, sometimes followed by fighting, maintain the hierarchy of dominance that pervades many primate troops. Such behavioural flexibility has taken the place of further physical specialisation.

A large brain requires a large brain case, or **cranium**, and in humans more of the skull is used in housing the brain than in the other apes. As a consequence, the brow tends to be vertical and lacks the prominent brow ridges possessed by the apes. These features, together with a shortening of the snout, have given humans a flat face, although the bones of the nose still protrude. For this reason, humans have a far more prominent nose than any other primate.

The brains of early **hominins** have not been fossilised, but because the brain fills the whole of the cranium, brain size can be determined by measuring the volume inside the cranium using an **endocast**. This capacity is known as **cranial capacity**.



Activity 12.1
Comparing primate skulls

Mobility of the digits

The limbs of primates tend to be unspecialised in structure, which allows for great diversity in their use. They are **pentadactyl**, which means they have five digits on each limb. The digits are highly mobile, a feature that can be related to the arboreal way of life of primate ancestors. Grasping, or **prehensile**, digits were essential for climbing by wrapping the long, curved digits around the branches of trees.

The evolutionary trend is towards increasing ability to move the digits independently of one another. The most highly developed digits in this respect are the thumb and the big toe. Not only are they independent, but they are also opposable in most primates. **Opposability** means that the first digit can be moved in such a way that it can touch each of the other digits.

The degree of opposability varies from species to species and depends on the relative length of the first digit compared with the other four. Almost all species of primate show some opposability of the big toe, with humans being the one notable exception. Our big toe is not opposable at all. Opposability was lost when the human foot became a weight-bearing, rather than a grasping, appendage. However, humans do possess the longest thumb of all primates and this has contributed considerably to our ability to manipulate objects with our hands.

Having highly mobile digits has enabled humans, more than any of the other primates, to manipulate objects with great skill. The human hand is short and broad, with short, straight fingers and a long, strong thumb, compared

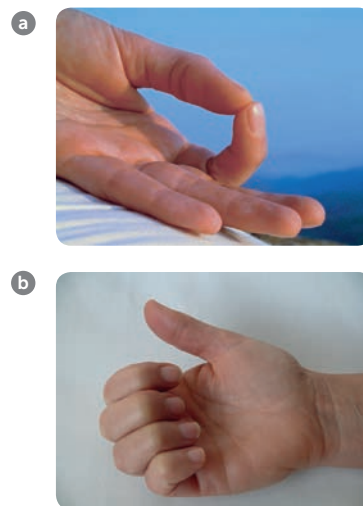


FIGURE 12.4
Manual dexterity of the human hand: **a** Opposability of the thumb as it moves across the palm to touch the other digits; **b** Prehensile digits are capable of being wrapped around an object – here the fingers are being curled towards the palm of the hand

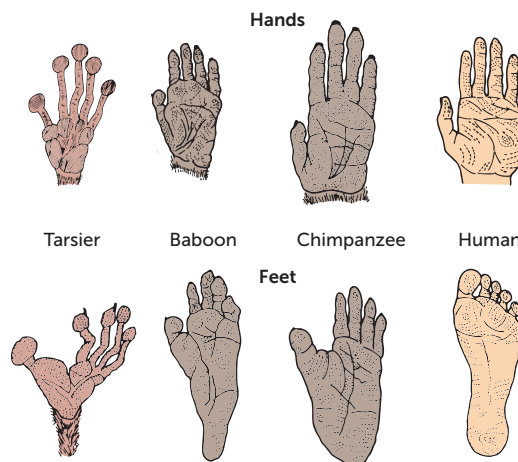


FIGURE 12.5 Hands and feet of four primates. Unlike other primates, humans do not have an opposable big toe

**Activity 12.2**

Observing the mobility of the human thumb

with that of the other primates. This arrangement gives the thumb a great degree of freedom, and it can readily oppose each of the other digits, thumb tip to fingertip, allowing humans to grasp objects with precision. The **precision grip**, such as that used for holding a pencil when writing, or a needle when sewing, is one of the hallmarks of being human, although it is not unique to humans. What is unique, however, is the amount of contact between the index finger and thumb. This enables humans to handle small or delicate objects effectively. It is different from the **power grip**, which happens when the thumb and fingers apply force against the palm.

The precision grip requires the presence of a truly opposable thumb and is also seen in Old World monkeys, particularly the ground-living baboons, mandrills and macaques. These monkeys are second only to humans in their manipulative abilities.



FIGURE 12.6 The **a** power and **b** precision grips

Left: Shutterstock.com/Ruslan Kudrin; right: Shutterstock.com/cunaplus

Locomotion – adaptations to bipedalism and quadrupedalism

Species in the family Hominidae include humans, chimpanzees, gorillas, orangutans and bonobos. During evolution, there has been a change from **quadrupedalism** (walking on four limbs) to **bipedalism** (walking on two legs). This is a major distinguishing feature of hominins and is used by scientists when classifying fossils.

For humans to be able to stand on two legs and walk bipedally with a striding gait, the skeleton and muscles had to evolve. Compare the skeletons of the gorilla and human in Figure 12.8. The differences seen have evolved over millions of years, so that present-day humans can stand and walk erect on two legs. This **adaptation** helped our human ancestors to survive, and hence has acted as a selective pressure during natural selection.

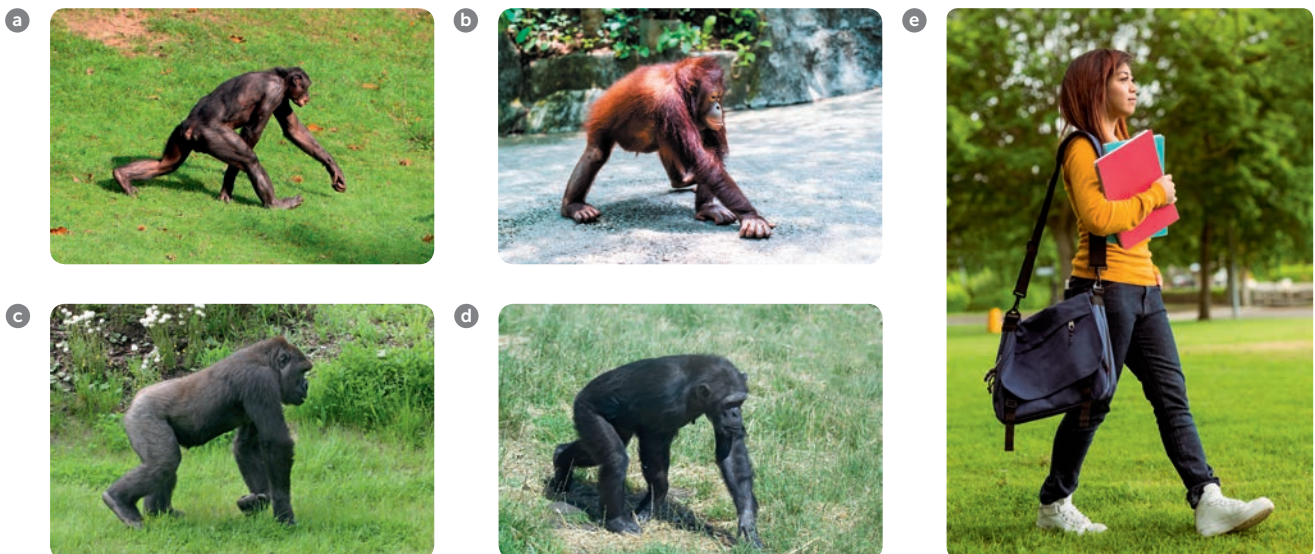


FIGURE 12.7 The evolutionary progression from quadrupedalism to bipedalism in **a** bonobo, **b** orangutan, **c** gorilla, **d** chimpanzee and **e** human

Clockwise from top left: Alamy Stock Photo/Ger Bosma; Shutterstock.com/ivMedvedeva; Shutterstock.com/wavebreakmedia; iStock.com/SoopySue; iStock.com/007_Bond

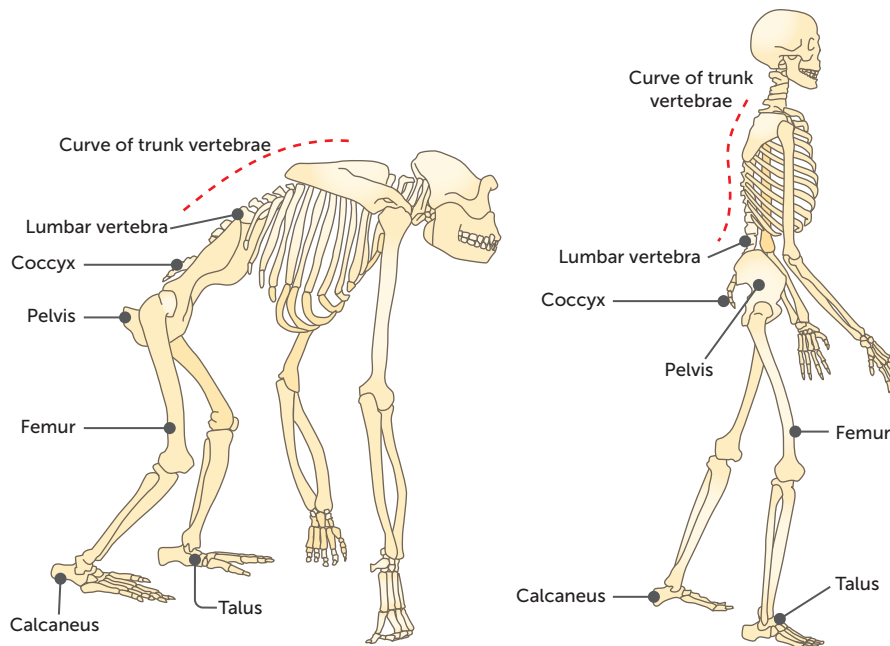


FIGURE 12.8 Posture of the skeletons of a gorilla and a human

Position of the foramen magnum

Where the brain joins the spinal cord there is a hole in the skull called the **foramen magnum**. During the evolution of modern humans from an ape-like ancestor, the foramen magnum has gradually moved forward to become more central. This allows the skull to balance on top of the vertebral column. An ape like a gorilla needs large neck muscles to hold the head in position. In humans, the weight of the skull is borne by the vertebral column and so large neck muscles are not required.

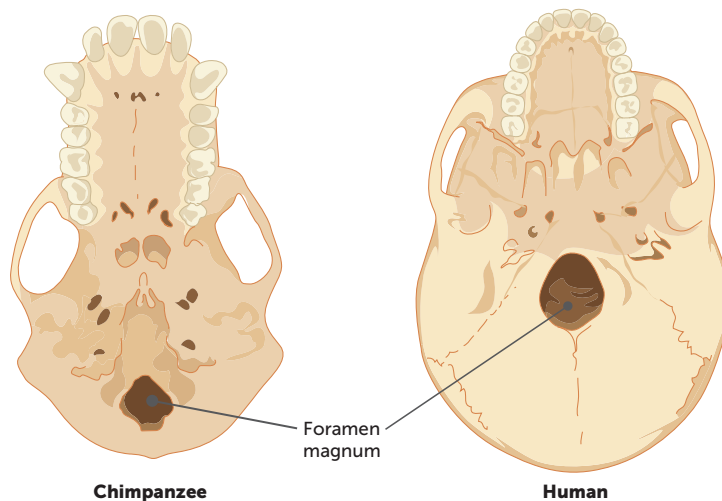


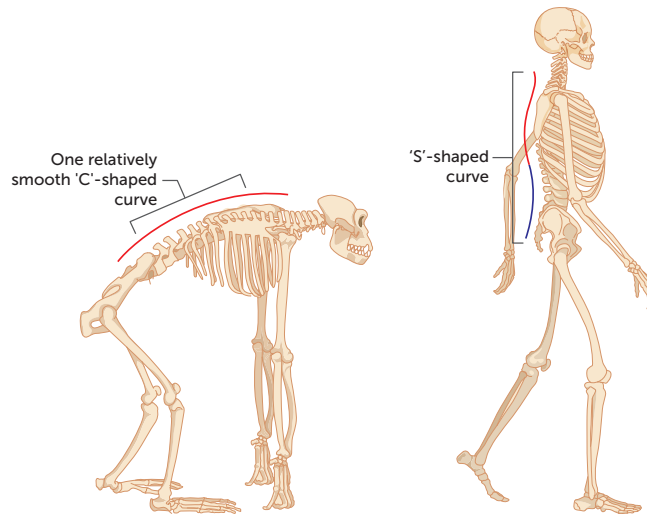
FIGURE 12.9 Base of a chimpanzee skull and a human skull, showing the position of the foramen magnum

Curvature of the spinal column

During evolution, the curvature of the spine has changed to allow an upright posture. The smooth 'C'-shaped curve seen in the spines of apes such as gorillas has evolved to an 'S'-shaped curve in humans. This improves the body balance in the upright position and enables the head to balance on top of the neck.

In humans, the double curvature is achieved by the vertebrae in the lower, or **lumbar**, region being wedge-shaped from front to back, thus forming a forward-jutting curve. In addition, the cervical curve in the neck brings the vertebral column directly under the centre of gravity of the skull.

FIGURE 12.10 The progression of a smooth C-shaped curve in a chimpanzee to an S-shaped curve in humans



The jaw

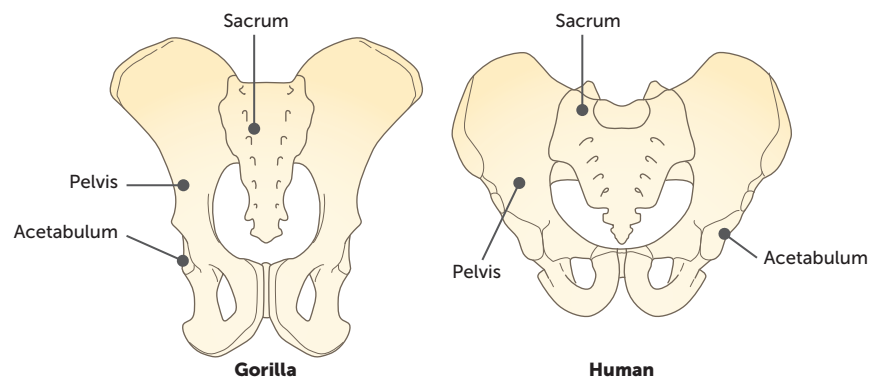
Apes have a protruding jaw, known as **prognathism**, whereas in humans the facial profile is much flatter. During evolution from an ape-like ancestor, the size and protrusion of the human jaw has gradually been reduced. This change has been important in allowing the skull to balance on the top of the spine, because the weight in front of the foramen magnum is approximately equal to the weight behind it. Balance is thus achieved with a minimum of muscular effort.

The pelvis

At its lower end, the vertebral column articulates with the pelvis. The pelvis in humans is broader, and shorter from top to bottom, than in apes, and bowl-shaped (Figure 12.11). This bowl shape supports the abdominal organs when standing erect, provides greater stability for bipedal locomotion and, in the female, supports the developing foetus during pregnancy. The female pelvis tends to be slightly broader than that of the male to allow for the passage of the infant at birth.

The broad hip bones provide space for attachment of the large buttock muscles, which move the legs and keep the upper body erect.

FIGURE 12.11 Pelvises of a gorilla and a human



The carrying angle

In humans, the shape and orientation of the pelvis result in the hip joint being directly under the trunk and head. This allows the weight of the body to be transferred from the pelvis to the legs. The head of the **femur**, or thigh bone, is large and fits into the **acetabulum** (hip socket) of the pelvis. Because the pelvis is broad, the hip sockets are wide apart, but the femurs tend to converge towards the knees. This arrangement of the femurs forms an angle to the vertical, termed the **carrying angle**, which ensures

that weight distribution remains close to the central axis of the body when walking. As Figure 12.12 indicates, in humans the weight tends to fall through the outside of the femur, whereas in other apes the reverse is true.

The carrying angle allows for greater stability in an upright posture. When walking, it enables the body to be rotated about the lower leg and foot, and each footstep follows a more-or-less straight line. This enables humans to have a striding gait instead of swaying from side to side as do gorillas or chimpanzees when walking on two legs.

The knee

In bipedal species, the weight of the body is transmitted down the outside of the femur to the knee. The knee joint is a two-part hinge joint, with one 'hinge' on either side of the ligaments in the middle of the joint. Because the weight is transmitted to the outer 'hinge', it is larger and stronger than the inner one. Although the weight of the body is transmitted down the outside of each leg, the centre of gravity of the body tends to fall through a line just in front of the knees. This results in a force that tries to bend the knee backward but is resisted by the ligaments making up the knee joint. This natural resistance produces a joint that requires no energy to support the body in a standing position.

The foot

From the knee joint, most of the weight of the body is transmitted through the tibia to the ankle. The tibia is the larger and stronger of the two lower leg bones. At the ankle, body weight is transmitted from the tibia through the talus (ankle bone) to the other tarsal bones, then to the metatarsals and phalanges via the arches of the foot.

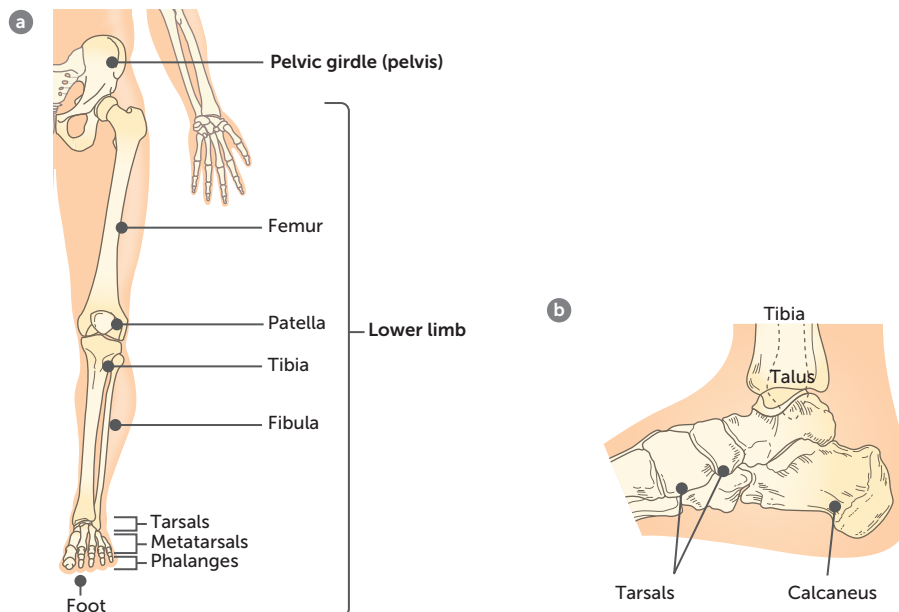


FIGURE 12.12 Pelvises and femurs of chimpanzees and humans, showing how humans have a carrying angle, with the femur angled in towards the knee (the dotted line shows the direction of weight transmission)

FIGURE 12.13 **a** Lower limb showing the weight-bearing bones; **b** Tarsal bones of the foot

The human foot is one of the most distinctive adaptations for bipedal locomotion. In becoming a highly specialised locomotory organ it has lost its grasping ability, or prehensility. This is most noticeable with the big toe, which in humans is quite large and aligned alongside the other toes. The bones of the foot between the toes and the ankle, the **metatarsals**, are shaped in such a way that they form two arches: a **longitudinal arch** running from front to back, and a **transverse arch** running from side to side.

The transverse arch is unique to humans. These two arches have enabled humans to perfect bipedal locomotion.

Centre of gravity

Unlike other apes, humans have legs that are longer than the arms. The relatively long legs increase the length of the stride when walking. Surprisingly, they also serve to lower the centre of gravity of the body, the point at which all the weight of the body appears to be concentrated. In contrast to humans, where almost half the total height is in leg length, in apes only about one-third of the total height is taken up in leg length. This results in their centre of gravity being further up the body. Whereas the centre of gravity for the ape is at chest level, for humans it is at the level of the pelvis. The lower centre of gravity in humans contributes to stability when moving bipedally or when standing erect.

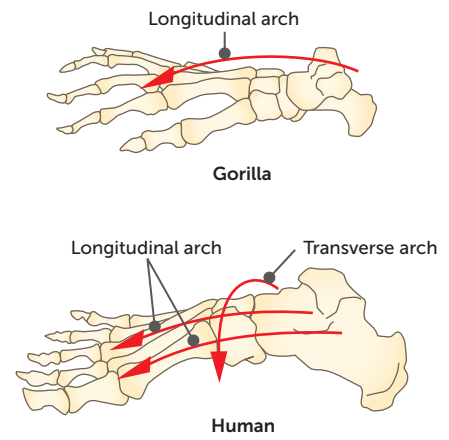


FIGURE 12.14 Arches of the foot of a gorilla and a human: humans have a longitudinal arch and a transverse arch; gorillas have only the longitudinal arch

Muscle tone

One of the essential elements for maintaining an upright stance is muscle tone. **Muscle tone** is the partial contraction of skeletal muscles. For example, to keep the head erect and stop it from slumping forward on to the chest, the muscles in the back of the neck are partially contracted; that is, they have tone. If someone falls asleep while sitting up, the decrease in tone is evident as the head nods until the chin is close to the chest.

Sustained muscle tone is most evident in those muscles that support the body in an upright position. In humans, the muscles that do this are those that bring about movement of the spine, hip, knee and ankle, and also the abdominal muscles. The nervous system and a variety of sense organs work together to maintain the tone in these muscles and the equilibrium of the body.

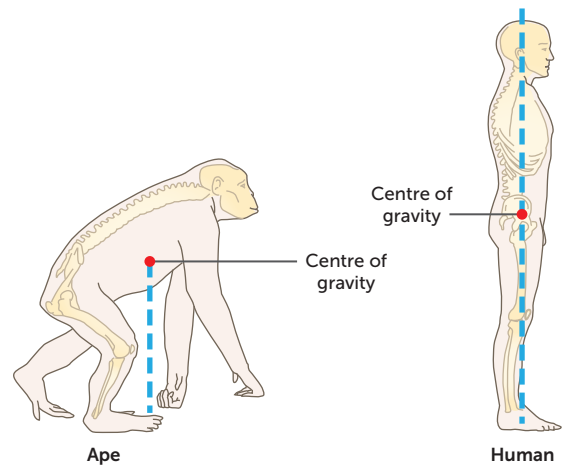


FIGURE 12.15 Centre of gravity of an ape and a human



Walking on two legs – bipedalism
This website has more information about bipedalism.



12.1 Adaptations for erect posture

TABLE 12.3 Summary of the main hominin adaptations for erect posture

STRUCTURE	ADAPTATION
Foramen magnum	Located centrally in the base of the cranium
Jaw bone	Small and non-protruding, enabling the skull to balance on the vertebral column
Vertebral column	Lumbar vertebrae wedge-shaped, producing an 'S'-shaped curve that brings the vertebral column directly under the centre of the skull
Pelvis	Broad; shallow from top to bottom. Provides support for the abdominal organs. Attachment of femurs is wide apart, contributing to the carrying angle
Femurs	Large head of the femur contributes to carrying angle
Knee joint	Outer 'hinge' larger and stronger, to take weight of body. Knee is able to be straightened
Legs	Longer than arms, contributing to a low centre of gravity. Carrying angle allows the weight of the body to be kept close to the central axis
Foot	Large heel bone and aligned big toe form a pedestal on which the body is supported. Foot has both longitudinal and transverse arches
Muscle tone	Partial contraction of muscles to support the spine, hip, knee and ankle

Key concept

Evolution has led to changes that allow bipedalism in humans. These changes include a central foramen magnum, 'S'-shaped spine, non-protruding jaw, broad pelvis, carrying angle of the femur, knee that is larger on the outside, long legs, longitudinal and transverse arches on the feet, and muscle tone.

Striding gait

Walking upright in such a way that the hip and knee are fully straightened is referred to as the **striding gait**. Hominins are the only animals that have perfected this form of locomotion. Even when walking on their hind legs, the other apes have their knees bent and their bodies bent forward at the hips.

In the striding gait, when the foot hits the ground, weight is transmitted from the heel along the outside of the foot as far as the ball, crosses the ball of the foot (via the transverse arch) and is finally borne by the big toe. At the final moment of striding, the whole weight of the body is propelled by the big toe. This is why the hominins lost the opposability of the big toe; the human foot has evolved into a weight-bearing appendage, rather than a grasping one.

When walking, the trunk rotates about the pelvis. The forward swinging of the arms compensates for this natural rotation of the body: the right arm naturally swings forward as the left leg is extended, and vice versa. Swinging of the arms tends to keep the shoulders at right angles to the direction of travel, and reduces the amount of energy expended. If the arms did not move as they do, energy would be wasted in reversing the rotation of the body after each stride.

In the discussion of the carrying angle earlier in this chapter it was shown that, although the human pelvis is broad and the hip sockets are wide apart, the femurs converge towards the knees. This arrangement of the femurs ensures that weight distribution remains close to the central axis of the body during walking. The arrangement also allows for stability during walking, as the body can be rotated about the lower leg and foot, thus allowing each footstep to follow a more-or-less straight line. Apes such as chimpanzees lack a wide pelvis and carrying angle. When walking on two legs they must sway from side to side so that the body weight is over each leg in turn.

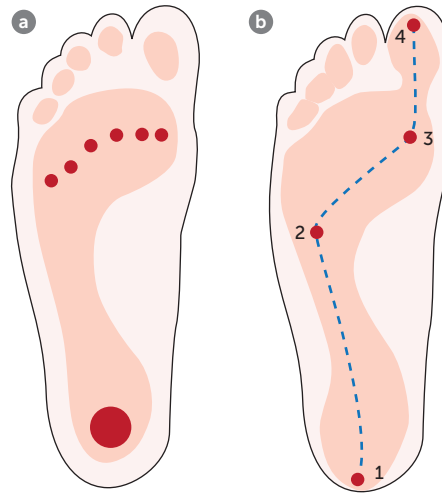


FIGURE 12.16 **a** How body weight is borne by the foot when standing still; **b** The distribution of body weight as a step is taken: the weight of the body is progressively borne on points 1 to 4 as the heel of the foot hits the ground and the big toe thrusts off

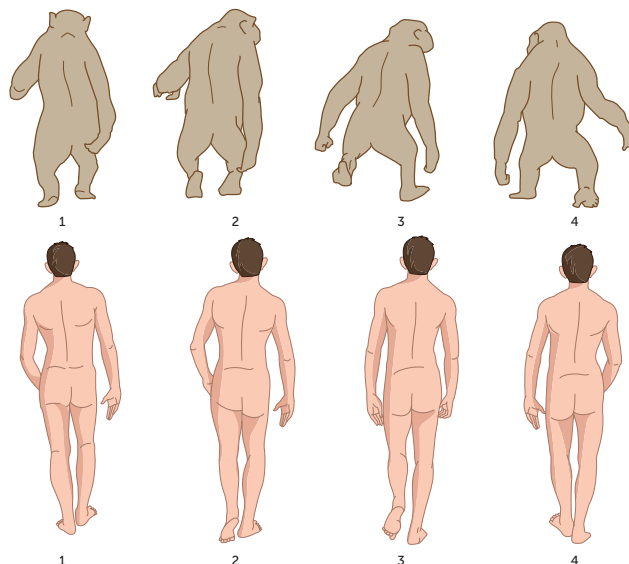


FIGURE 12.17 Comparison of the bipedal walking of a chimpanzee and a human

Advantages of bipedalism

Evolutionary trends arise due to a selective advantage leading to natural selection. In the case of bipedalism, there are a number of possible advantages, including:

- It is a more energy-efficient means of moving.
- It leaves the hands free to use tools.
- It leaves the hands free to carry items.
- The upright stance achieves greater height and thus the ability to see further.
- The upright stance means that less of the body is exposed to sunlight.
- The upright stance increases exposure to breezes, increasing cooling mechanisms.



Activity 12.3

Investigating upright stance and the striding gait

Key concept

Humans have a striding gait due to the carrying angle of the femur and the weight-bearing ability of the big toe. This allows humans to have their weight on one foot without twisting or swaying.

Prognathism and dentition

Evolutionary changes have taken place in the dentition of the primates, in both the number of teeth and in their structure. As with most mammals, primates have two sets of teeth, deciduous (also known as baby teeth) and permanent, and teeth of different shapes that perform different functions.

Number and shape of teeth

The number of each type of tooth that a species has can be expressed as a **dental formula**.

The formula gives the number of each type of tooth in one quarter of the jaw. Primitive mammals had a dental formula of 3:1:4:3. This means that there are 44 teeth: three incisors, one canine, four premolars and three molars on each side of each jaw.

Natural selection has resulted in a decrease in the number of teeth in primates compared with early mammals. This is probably related to the gradual reduction in the size of the face and jaw that has occurred in primates that allows the skull to balance during bipedalism. Old World monkeys, apes and humans all have 32 teeth and a dental formula of 2:1:2:3; however, there is considerable difference between them in the structure and arrangement of the teeth.

In the Old World monkeys and apes, the canines are usually large and sharply pointed, projecting beyond the level of the other teeth. Such large canines have required modifications to adjacent teeth

FIGURE 12.18 **a** The diastema is a gap between teeth that allows the teeth on the opposite jaw to fit in; **b** A jaw without a diastema has the teeth close together



Left: Alamy Stock Photo/Nature Picture library; right: Shutterstock.com/Sergey Furtaev

so that the mouth can be closed. Most primates with large canines have a gap, or **diastema**, between the upper second incisor and the upper canine to accommodate the large lower canine. To allow for the large upper canine, the crown of the first lower premolar is slanted back and has a sharp edge. The upper canine fits tightly against this premolar and is sharpened by the grinding that occurs.

The surface of the molars of apes and humans has evolved from the three cusps of early mammals to four cusps on the upper molars and five cusps on the lower ones. This pattern has been useful in identifying the teeth of fossil apes and humans, and is presumed to have evolved due to the predominantly fruit diet of the apes.

Compared with other primates, human dentition is very distinctive. In humans the canine teeth do not project beyond the level of the other teeth and interlock, as they do in the Old World monkeys and apes. They are more even in size, looking more like incisors. These small canine teeth and relatively small incisors take up less room in the jaw. As a consequence, the shape of the tooth row, or **dental arcade**, has evolved into a different shape. Instead of the 'U' pattern of the apes, it has become parabolic in shape, as shown in Figure 12.20.

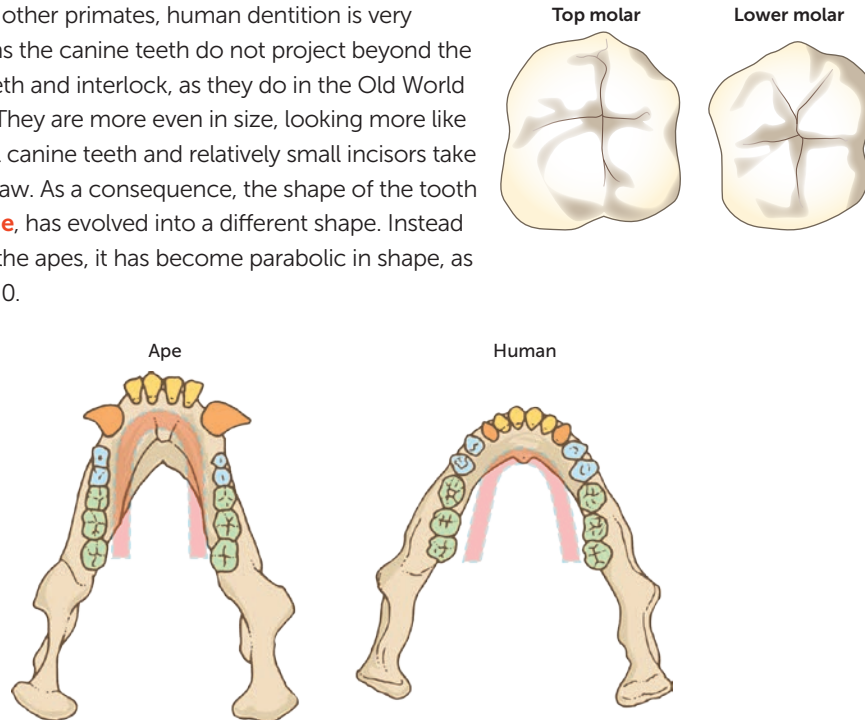


FIGURE 12.19

The difference in structure between a four-cusp and a five-cusp tooth. The 'valleys' between the four cusps of the top tooth form a '+' pattern, while the 'valleys' between the five cusps of the lower tooth form a 'Y'



Primate teeth

This website provides more information on primate dentition.

FIGURE 12.20 Dental arcade of a non-human ape and a human

Prognathism and brow ridges

Non-human apes and the early hominins have a forward-jutting jaw, a characteristic known as **prognathism**, and a distinct **brow ridge**, the bony ridge located above the eye sockets, very evident in adult gorillas. With evolution, the tooth size gradually decreased leading to a flattening of the face, development of a chin and a prominent nose. With the move to bipedalism, a flatter face shifts the weight to a more central position, allowing the skull to balance during an upright stance. And as the size of the frontal lobe has increased, the brain occupies a larger volume, extending the cranium forward and reducing the brow ridges.



Alamy Stock Photo/Sabena Jane Blackbird

FIGURE 12.21

Prognathism is the forward protrusion of the jaw

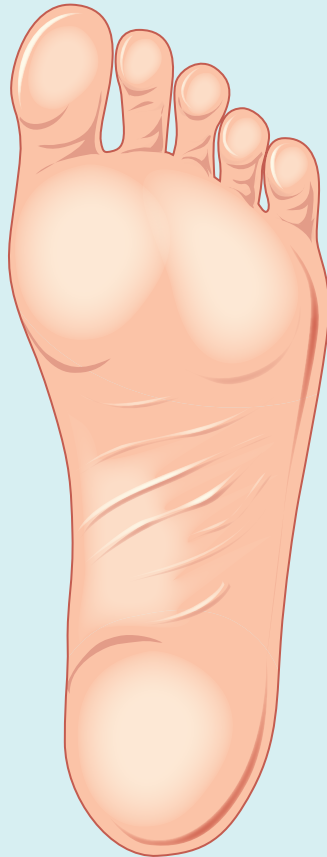
Key concept

During the evolution of primates, the diastema has been lost, the number of teeth and prognathism have decreased, the number of cusps on the molars has increased, and the jaw has become more parabolic in shape.

Questions 12.2

RECALL KNOWLEDGE

- 1 What family are humans in?
- 2 List six characteristics of hominids.
- 3 Describe the trend in the cerebral cortex that has occurred during evolution.
- 4 Define 'pentadactyl' and 'opposable'.
- 5 Use an example to describe:
 - a precision grip
 - b power grip.
- 6 What is meant by 'bipedal with a striding gait'?
- 7 List the features that allow humans to have a striding gait.
- 8 Explain why a bowl-shaped pelvis in humans has an advantage for bipedalism over the longer pelvis of other apes.
- 9 Define 'carrying angle' and explain why it allows a striding gait.
- 10 Which side of the knee is larger? Explain why.
- 11 Describe the distribution of weight from the hip to the foot of a human.
- 12 Draw the transverse and longitudinal arches on the diagram of a foot below.



- 13 Describe the trend in prognathism during evolution.
- 14 State the dental formula of hominids.

APPLY KNOWLEDGE

- 15 Explain the significance of an increase in the size of the frontal lobe.
- 16 Which animal would have a more convoluted cerebrum – an orangutan or a chimpanzee?
- 17 Explain the difference between the size of the brain and the cranial capacity.
- 18 Explain how the length of the thumb of humans reflects a greater degree of evolution.
- 19 The spine of humans is described as 'S' shaped. Explain why this is necessary for bipedalism.
- 20 Explain why doctors are reluctant to amputate the big toe.
- 21 Gorillas have a diastema, but humans do not. State what a diastema is, and explain why it is present in the jaw of gorillas but not humans.
- 22 Explain why bipedalism would have allowed 'survival of the fittest' during natural selection.

CHAPTER 12 ACTIVITIES

ACTIVITY 12.1 Comparing primate skulls

In this activity, you will use a website to compare a number of primate skulls, observing trends in the size and shape of the skull and teeth as one goes from the lemurs and monkeys to apes and humans.

What to do

- 1 Go to the weblink 'eSkeletons'.
- 2 Select 'Comparative Anatomy' from the menu at the top. This will enable you to compare two different species of primate.
- 3 In the comparative anatomy screen, select 'Adult Male Baboon' and 'Adult Male Orangutan' from the Specimen column; then from the Bone column select Cranium, and select 'Lateral' from the View column.
- 4 You should now have the lateral (side) view of an orangutan and a baboon skull next to each other to compare. Click on the + sign above the images to increase their size.
- 5 Look carefully at the two skulls, noting the scale listed for each, and take this into consideration when answering the following questions. For some questions it may help to go back and select other views of the skulls for comparison.
 - a Using the scale provided, estimate the length of each skull.
 - b Which skull has a more rounded profile?
 - c Estimate the length of the cranium of each skull. Which species would have the larger and more complex brain? Give reasons for your answer.
 - d Identify and count the teeth that are visible. What is the dental formula for each species?
- 6 Repeat steps 3 to 5 so that you can compare:
 - a an orangutan with a gorilla
 - b a gorilla with a chimpanzee
 - c a chimpanzee with a human.

Studying your observations

Review your answers to the questions and use the information collected to describe evolutionary trends in the size and shape of the skull and teeth from baboons to humans.



eSkeletons

ACTIVITY 12.2 Observing the mobility of the human thumb

Apes and humans have very mobile digits, but only humans can grip an object with true precision. The human hand differs structurally and functionally from that of the other primates. A longer, stronger thumb that can readily oppose each of the other digits enables humans to manipulate objects using a precision grip. Humans are also able to use a power grip, where an object is grasped between the undersides of the fingers and the palm of the hand, with pressure in the opposite direction being applied by the thumb. We use a power grip when holding a hammer.

In this activity, you will compare the two main ways in which humans use the thumb and fingers to grip objects. Manipulation of objects with both power and precision enabled our ancestors to become efficient tool makers.





You will need

A short length of broom handle or a ruler; a pencil or pen

What to do

- 1 Hold your hand out in front of you with the back of your hand towards your face. Observe how the position of the thumb is different from the fingers.
- 2 Move your thumb across the palm of your hand to touch each of your fingers in turn. Note the movement of the thumb.
- 3 Use your thumb and fingers to pick up a pen or a pencil from your table and hold it as though you are going to write. Observe the way in which the thumb and fingers are employed in the grip you used. This is the precision grip.
- 4 Using this grip, squeeze the pen tightly and note which muscles are in use.
- 5 Grasp a length of broom handle or a ruler as you would a hammer. Observe the differences in the position of the thumb and fingers when this method is used to hold an object.
- 6 Squeeze the broom handle tightly and note which muscles are used. This is the power grip.

Studying your observations

- 1 In relation to the palm of your hand, how is the position of the thumb different from the fingers? Give two reasons to explain the advantage of the thumb in this position.
- 2 What term is used to describe the movement of the thumb when it touches each fingertip in turn?
- 3
 - a Describe the position of your thumb and fingers when picking up a pen.
 - b Which muscles were used to hold the pen in this precision grip?
- 4
 - a List the differences in the position of the thumb and fingers when using the precision grip and the power grip.
 - b How did your thumb assist in holding an object in the power grip? Describe how it did this.
 - c Which muscles were employed in the power grip? Were these different from the ones used in the precision grip?
- 5 Which of the two grips would be the most efficient at holding an object against force?
- 6 List the features of the thumb that make both the power and precision grips possible.

ACTIVITY 12.3 Investigating upright stance and the striding gait

A striding gait is a form of locomotion that distinguishes humans from the other living primates. Its evolution depended on changes to the skeleton and associated muscles and joints. In this activity, you will examine some of these features to gain a greater understanding of the way we move.

You will need

A model of a human skeleton; charts or diagrams of the skeleton; the skull of an ape; reference to some of the diagrams in this book. If you wish, you could do the whole activity by comparing the human skeleton with that of the chimpanzee or gorilla at the weblink from Activity 12.1.

What to do

Answer the questions below. As you answer them, refer to the model of the human skeleton, ape skull and figures in the text as directed, or to images on a website.

Studying your observations

- 1 Compare the skull of an ape with that of a human. List the differences in the size and shape of the crania (brain cases).



-
- 2 Locate the position of the foramen magnum. Look at the base of each skull and compare the position of the foramen magnum in the ape and in the human. Where is the foramen magnum in the human skull? Where is the foramen magnum in the ape skull?
 - 3 Which skull is most easily balanced on the vertebral column: ape or human?
 - 4 Look carefully at the model of the skeleton, and then refer to Figure 12.10. Describe the curves of the vertebral column of the ape and the human. What extra curve exists in the vertebral columns of humans?
 - 5 Look at Figure 12.11 and compare the shape of the human pelvis with that of the gorilla. Which pelvis is wider? Which is longer? Suggest reasons for the relatively wide pelvis in humans.
 - 6 The human pelvis is tilted forward and curves inward, creating a basin shape. List the advantages this arrangement has for upright stance.
 - 7 Look carefully at the model of the skeleton again, and then refer to Figure 12.12. The narrow pelvis of the ape makes the legs hang vertically. This means the ape must keep its feet apart when standing and, when walking, sway from side to side to maintain balance. Describe how the breadth of the pelvis contributes to the carrying angle of the femurs.
 - 8 Explain the effect of the carrying angle on the arrangement of the knees, lower limb bones and the position of the feet in humans. What advantage does this arrangement have for a human walking?
 - 9 The vertebral column of humans acts as a weight-supporting column. How does the shape of the lumbar vertebrae contribute to the lumbar curve? Look closely at the angle between the lumbar curve and the pelvis. What effect does the lumbar curve have on the position of the trunk and legs in humans?
 - 10 Refer to Figure 12.15 and compare the position of the centre of gravity in humans and apes. Which animal has the lower centre of gravity relative to body size? What features of the skeleton contribute to this difference?
 - 11 Describe the pathway the body weight in humans follows from the pelvis down to the feet.
 - 12 Remove your shoe and run your fingers over the top of your foot from little toe side to big toe side. Can you feel the transverse arch? How is this arch different from the longitudinal arch? What is the main function of the two arches?
 - 13 Look at the model of the skeleton again, and then refer to Figure 12.14. Compare the toes of a gorilla and a human. What differences can you see?
 - 14 When humans stride, the big toe provides the thrust. What features of the big toe assist this? Would an ape be able to use the big toe in a similar way? Explain your answer.
 - 15 Describe how the arches of the foot enable weight to be distributed from the heel to the big toe. Remove your shoes and try this for yourself.
 - 16 Take a number of steps in your bare feet. Describe what occurs from the time your left heel hits the ground until your right heel hits the ground. Referring to Figures 12.16 and 12.17 may help you with your description.
 - 17 Summarise the main features in the human skeleton that are adaptations for an upright stance and for walking bipedally with a striding gait.

CHAPTER 12 SUMMARY

- Humans are primates, and are in the same family as chimpanzees, bonobos, gorillas and orangutans. This family is called Hominidae, and the species are referred to as hominids.
- Primates have unspecialised bodies and limbs, five fingers and toes with nails instead of claws and an opposable first digit, forward-facing eyes, poor sense of smell, and a large and complex brain.
- Humans have a recent common ancestor with chimpanzees and gorillas, and a slightly more distant common ancestor with orangutans.
- Hominids share common features, including larger, more complex brains, five cusps on the molar teeth of the lower jaw, freely rotating arms, a wide, shallow chest, no external tail, an appendix and are active during the day.
- The size of the brain, especially the cerebral cortex, has increased during evolution. Humans have larger brains with more convolutions when compared to the other apes. This has allowed more advanced behaviours, such as tool making.
- As brains are not fossilised, the size of the brain is determined by the cranial capacity – the volume inside the cranium.
- As primates have evolved, the degree of opposability of the thumb and big toe (with the exception of humans) has increased. This has led to a precision grip in addition to the power grip.
- During evolution, there has been a change from quadrupedalism to bipedalism, with humans walking on two legs with a striding gait. Adaptations that allow bipedalism are:
 - central foramen magnum
 - S-shaped curve (double curve) of the spine
 - flatter facial profile with reduced protrusion of the jaw
 - a broad, shorter pelvis
 - femurs forming a carrying angle with the vertical line
 - knee joints that are larger on the outside and contain ligaments that resist the force acting on the knee
 - a tibia that is larger than the fibula
 - big toes that are non-opposable
 - both a longitudinal and a transverse arch in the feet
 - legs that are longer than the arms, lowering the centre of gravity
 - muscle tone to support the body.
- Bipedalism provided a number of advantages that led to a greater chance of survival during natural selection and, therefore, to its being passed on to future generations.
- A striding gait occurs when the hips and knees can be fully extended. Hominins (humans) are the only species that are able to do this.
- In a striding gait the weight is transferred from the heel along the outside to the ball of the foot, and then across to the big toe. The trunk rotates, and this is balanced by the swinging of the arms. At the same time, the carrying angle of the femur keeps the weight close to the central axis.
- Through evolution of hominids, the teeth and jaw have changed so that humans do not have a diastema, and do have smaller canines and incisors and a parabolic dental arcade. There has also been a reduction in prognathism and the size of the brow ridge.

CHAPTER 12 GLOSSARY

Acetabulum The socket of the pelvis in which the head of the thigh bone fits

Adaptation A particular structure, physiological process or form of behaviour that makes an organism better able to survive and reproduce in a particular environment

Bipedalism Walking on two legs

Brow ridge A ridge of bone above the eye sockets of the skull

Carrying angle The arrangement of the thigh bones to form an angle to the vertical

Cerebral cortex The outer layer of the cerebrum, made up of grey matter

Cerebrum The largest part of the brain; made up of left and right hemispheres

Convolution An upward fold of the cerebral cortex of the brain; also called gyrus

Cranial capacity The volume of that part of the skull that is occupied by the brain

Cranium The part of the skull that contains the brain

Dental arcade The shape of the pattern made by the teeth as they are set in the jaw

Dental formula A formula that gives the number of each type of tooth in one-quarter of the jaw

Diastema A gap in a row of teeth; usually refers to a gap next to the canine teeth in primates, with canine teeth that are much longer than the other teeth

Diurnal Being active during the day

Endocast An impression of the inside of the brain case, either artificial or natural, made of rock or some other solid material

Femur The thigh bone

Foramen magnum The opening beneath the cranium through which the spinal cord passes

Frontal lobe One of the five lobes of each cerebral hemisphere

Hominid A member of the family Hominidae; includes humans and the other great apes (chimpanzees, gorillas, orangutans and bonobos)

Hominin A member of the tribe Hominini; humans, both past and present

Longitudinal arch The arch of the bones of the foot, running from front to back

Lumbar Describes the lower region of the spinal column; lumbar vertebrae support the lower back

Metatarsals The bones of the foot between the toes and the ankle

Muscle tone The partial contraction of skeletal muscles

Opposability The ability to use the thumb to touch the tips of each of the other digits on the hand

Pentadactyl Describes a limb with five fingers or toes

Power grip Force applied by the fingers and thumb towards the palm to transmit force to an object

Precision grip The grasping of an object between thumb tip and fingertip, as in holding a pencil when writing

Prehensile Grasping; refers to the digits of a hand or a foot that can grasp an object

Prognathism Having a protruding jaw

Quadrupedalism Walking on four legs

Striding gait A way of walking in which the hip and knee are fully extended

Transverse arch The arch of the bones of the foot, running from side to side

CHAPTER 12 REVIEW QUESTIONS

Recall

- 1 To which of the primate families do humans belong? Who shares this family with us?
- 2 Describe the evolutionary trend evident in primates concerning the mobility of the thumb and the other digits.
- 3
 - a List the components of the skeleton that allow humans to adopt an erect posture.
 - b How do these components differ from the corresponding ones in a quadrupedal animal?
 - c What are the advantages and the disadvantages of an erect stance and bipedal locomotion?
- 4 Describe carrying angle, and compare the carrying angle of an ape with that of a human.
- 5 How does the wide pelvis and carrying angle of the femur enable humans to walk without the body swaying from side to side?
- 6 What is an endocast? What can it tell us about the size and shape of the brain?
- 7 Describe the major anatomical and functional developments that have occurred in hominid brains over the past four million years or so.
- 8 Describe the change in the shape of the face of hominids over the past four million years or so.

Explain

- 9 Explain how muscle tone helps to support the body against the force of gravity.
- 10 When we walk, our arms move in a coordinated way. Explain how arm movement helps stabilise the body of a human while walking.
- 11 Human dentition is said to be unique.
 - a List the differences between the teeth of a human and those of an ape, such as a gorilla.
 - b How has the dental arcade changed in hominins compared with that of an ape?

Apply

- 12 Chimpanzees have been observed using a range of simple tools, mainly associated with feeding. Describe the structural characteristics of chimpanzees that enable them to make and use tools.
- 13 For humans to be able to stand upright, a number of adaptations have taken place. Changes have occurred to the skull, vertebral column, pelvis, legs and feet. Describe how each of these has contributed – and how they have interacted – to enable humans to adopt an erect stance.
- 14 If you have seen chimpanzees or gorillas walking bipedally, you will have noticed that they sway from side to side as they walk. Explain why they cannot stride as humans do.
- 15 What assumptions are made when scientists infer the degree of intelligence from the cranial capacity of a skull?
- 16 The human canine tooth is much smaller than that of the other hominids, especially in the males of the species. Describe the evolutionary processes that would have taken place in hominins to produce the current size of that tooth in humans today.
- 17 Briefly describe how the environment could have contributed to the first hominins evolving the free striding gait. How would this gait have increased the chance of survival in that environment?

Extend

- 18 As a result of various conditions, the normal curves of the vertebral column may become exaggerated. Use references to describe the conditions known as scoliosis, kyphosis and lordosis.
- 19 The term 'hominid' used to have the same meaning that 'hominin' now has. 'Hominid' was used to refer to the various members of the human family tree. Scientists who study human origins

have changed the classification scheme by introducing a new level, the tribe. 'Hominid' is now defined in a much broader way so that it refers to all great apes and their ancestors. 'Hominin' refers only to present-day humans and our extinct ancestors. Why would scientists make changes to the classification scheme for apes and humans? Suggest as many reasons as you can.